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FISONOMIA Y COMPOSICION DE LA VEGETACION SECUNDARIA EN UN AREA DE MATORRAL DEL NORESTE DE MEXICO

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RESUMEN

Se describen la fisonomía y la composición florística de la vegetación secundaria de cinco áreas ubicadas al sur del municipio de Linares, Nuevo León, México (con clima, suelo y topografía similares, pero con historiales de uso de suelo diferentes). Los resultados muestran una amplia diversidad fisonómica que incluye comunidades subarbustivas, arbustivo - arbóreas y mixtas, con una o varias especies dominantes. La composición florística está dada por 64 especies leñosas: 33 arbustivas y/o arbóreas y 31 subarbustivas, de 30 familias, de las cuales Leguminosae es la más importante entre las arbustivas y arbóreas, y Compositae entre las subarbustivas. Las especies más importantes en la vegetación secundaria de la región son: *Acacia rigidula*, *A. farnesiana*, y *Cordia boissieri*, entre las arbustivas y arbóreas; y *Lantana velutina*, *Gymnosperma glutinosum*, y *Croton cortesianus* entre las subarbustivas. La mayor similitud florística se presenta entre los predios que comparten la misma edad desde el último desmonte.

PALABRAS CLAVE: vegetación secundaria, fisonomía, matorral, Nuevo León, México

ABSTRACT

This paper documents physiognomy and floristic composition of the secondary vegetation in five stands in the southern part of Linares, Nuevo León, México (with similar climate, soil and topography, but different land use

history). Wide physiognomic diversity was found including one or several dominant species in subshubby, shrubby, and mixed communities. The floristic composition includes 64 woody species: 33 shrubs and/or trees and 31 subshrubs, of 30 different families. Leguminosae is the most important among shrubs and trees, and Compositae among the subshrubs. *Acacia rigidula*, *A. farnesiana*, and *Cordia boissieri*, are the main species among shrubs and trees; and *Lantana velutina*, *Gymnosperma glutinosum*, and *Croton cortesianus* are the most important subshubby species. Stands with similar age after clearing were closer regarding floristic composition.

KEY WORDS: secondary vegetation, physiognomy, thornscrub, Nuevo León, México

INTRODUCCION

Los procesos degradativos de origen antrópico de la vegetación en el noreste de México se remontan varios siglos atrás. Sin embargo, fue en la década de los setentas cuando dicha degradación se aceleró debido al Programa Nacional de Desmontes, el cual fomentó los desmontes de grandes áreas con vegetación natural para convertirlas en áreas de cultivo o en praderas artificiales. Este programa, sin embargo, no contempló la vocación natural del suelo ni dio seguimiento y apoyo financiero para que dichas áreas pudieran seguir siendo aprovechadas. Como consecuencia, muchas de ellas fueron abandonadas después de unos cuantos años y actualmente se encuentran ocupadas por vegetación secundaria.

En el noreste de México, las superficies ocupadas por áreas agrícolas y pastizales se han ido incrementando en los últimos años. En el municipio de Linares, Nuevo León, las superficies dedicadas a uso agrícola o pecuario intensivo en 1973 representaban un 37.5%, en 1980 un 37.9%, y en 1986 un 41.2%. Si a estas áreas se agregan las superficies que un algún momento fueron utilizadas para actividades productivas y que por diversas razones dejaron de utilizarse como tales dando origen a vegetación secundaria, la cifra aumenta a 52.2%, mientras que solamente un 45% permanece sin cambios radicales de uso (Treviño 1992, 1996).

Este artículo es el primero de una serie en la que se pretende dar a conocer los resultados del análisis de la vegetación secundaria de Linares, Nuevo, León, México, realizado como trabajo de tesis de maestría de la primera autora (González 1996). En esta primera parte se documentan la diversidad fisonómica y la composición florística.

AREA DE ESTUDIO

El área seleccionada para este trabajo se ubica al sur del municipio de Linares, Nuevo León, en el extremo oeste de la Planicie Costera del Golfo en el noreste de México. Las coordenadas geodésicas UTM (Universal Transversal de Mercator) que incluyen toda el área de estudio corresponden a 2729225 a 2741700 Norte y 438300 a

447520 Este (24° 40' 30" a 24° 47' 30" latitud Norte, y 99° 31' 00" a 99° 37' 00" longitud Oeste) (Figura No. 1).

La altura sobre el nivel del mar oscila entre 360 m y 420 m; el relieve es moderado, presentándose llanuras y pendientes suavemente onduladas entre 2 y 5%. Los tipos de suelo van de los típicos vertisoles pélicos y crómicos profundos de color oscuro y de origen aluvio-coluvial en las áreas bajas y sin pendiente, a los regosoles calcáricos, someros, en áreas con pendientes suaves.

Según la clasificación de Köppen, modificada por E. García para la República Mexicana, el clima del área es del tipo (A)C(w_o), que corresponde a un semicálido subhúmedo con lluvias principalmente en verano (20% de lluvia entre noviembre y abril) y presencia de un periodo de sequía interestival (canícula). La precipitación media anual es de 749 mm y temperatura media anual de 22.3° C, con temperaturas arriba de 40° C en el verano y heladas durante el periodo de diciembre a marzo.

El uso de suelo actual en la región corresponde a un mosaico de áreas agrícolas, pastizales inducidos, vegetación secundaria y áreas cubiertas de vegetación natural aparentemente primaria, en donde no existen evidencias de desmonte. Entre los fragmentos de vegetación aparentemente primaria, predominan los matorrales altos espinosos y subinermes, caracterizados por arbustos altos y árboles bajos. Este tipo de vegetación se podría ubicar, de acuerdo a la clasificación de Rzedowski (1978) como una transición entre el Matorral Xerófilo y el Bosque Espinoso.

METODOS

Selección de áreas de muestreo.

Mediante un análisis visual comparativo de imágenes de satélite LANDSAT de dos fechas (MSS, 17 de marzo de 1973; y TM, 11 de noviembre de 1988), uso de cartografía temática de la región, y exhaustivos recorridos de campo a través de todo el municipio de Linares, se seleccionaron cinco predios que actualmente presentan vegetación secundaria: Rancherías, La Loma, El Puerto, Santa Rosa, y Los Hoyos. Todos ellos comparten las mismas o similares condiciones físicas (clima, suelo, altitud, y pendiente), vegetación original (matorrales altos espinosos y subinermes), actualmente se utilizan en forma mínima o no se utilizan, comparten una edad entre 16 y 18 años después del desmonte o del cese de aprovechamiento, y cuando fueron desmontados se procedió también a desenraizamiento de las plantas. Difieren por otra parte en su historial de uso de suelo en el periodo de 1975 a la fecha. Dicho historial se clasificó en cinco tipos de acuerdo a:

- Fecha de último desmonte: reciente (Re), de 20 años o menos; ó antigua (An), de 25 años o más.
- Uso de suelo entre 1975 y 1977: vegetación primaria (Pri), vegetación secundaria (Sec), agricultura (Ag), pastizal (Pa).

- Uso de suelo entre 1978 y 1981: agricultura (Ag), pastizal (Pa), cese de aprovechamiento o abandono (Ab).

En la Tabla No. 1 se resumen las características de los diferentes historiales de uso reconocidos y se registran las claves con las que se refieren en el resto de este trabajo.

Sitios de muestreo.

*Se seleccionaron 21 sitios para muestreos cuantitativos: 6 en La Loma (L1 a L6); 7 en El Puerto (P1 a P7); 5 en Rancherías (R1 a R5); 2 en Los Hoyos (H1 a H2), y 1 en Santa Rosa (M1). La diferente cantidad de sitios seleccionados en cada predio obedeció al tamaño de los mismos y a la heterogeneidad de la cobertura vegetal detectada mediante el análisis visual de las imágenes de satélite, fotografías aéreas y recorridos preliminares sobre el terreno. Se evitaron los bordes de los predios (al menos 50 m). La ubicación exacta de los sitios de muestreo se obtuvo utilizando un receptor del Sistema Global de Posicionamiento (GPS).

Unidad muestral.

Se diseñó una unidad muestral de 360 m² compuesta por dos parcelas rectangulares proporción 1:10, de 4 m de ancho por 40 m de largo (160 m²) colocadas sobre el terreno en forma de escuadra de 90°. Una parcela con dirección Norte-Sur, y la otra con dirección Este-Oeste.

Registro de variables y colectas de material botánico.

Las variables registradas para todos los individuos de las especies arbustivas y arbóreas mayores de 0.5 m fueron: altura, dos diámetros de copa (medidos en dirección paralela y perpendicular a lo largo de la parcela, respectivamente). Para los individuos de las especies subarbustivas se consideró presencia.

Se elaboró una base de datos georeferenciados en la que cada registro representa un especímen vegetal muestreado. Dicha base de datos incluye 2,725 registros de arbustivas y arbóreas, y 4,068 de subarbustivas. El material botánico colectado durante los muestreos fue identificado y los especímenes quedaron depositados en el Herbario, CFNL de la Facultad de Ciencias Forestales de la Universidad Autónoma de Nuevo León (C.F.N.L.) en Linares, Nuevo León.

Estimación de parámetros básicos de la vegetación.

Para las especies arbustivas y arbóreas, en sus estratos medio y superior, se estimaron los parámetros básicos estructurales de la vegetación: densidad absoluta (D), cobertura aérea absoluta (C), y frecuencia absoluta local (F); así como los valores relativos de dichos parámetros: densidad relativa (DR), cobertura relativa (CR), y frecuencia relativa (FR). Se calculó además el valor de importancia (VI) de cada

especie por parcela. Para las especies subarbustivas solo se obtuvieron los valores de densidad.

Tabla No. 1. Historial de uso de suelo en los sitios de muestreo. RePriAg (sitios cuya vegetación primaria fue eliminada hace menos de 20 años para utilizarse temporalmente para agricultura); ReSecAg (sitios cuya vegetación secundaria fue nuevamente eliminada hace menos de 20 años para utilizarse temporalmente para agricultura); ReSecPa (sitios cuya vegetación secundaria fue nuevamente eliminada hace menos de 20 años para establecimiento temporal de pastizales); AnPaAb (sitios que fueron desmontados hace más de 25 años, utilizados temporalmente como pastizal y abandonados desde hace por lo menos 18 años); y AnAgAb (sitios que fueron desmontados hace más de 25 años, utilizados temporalmente para agricultura y abandonados desde hace por lo menos 18 años).

CLAVE	SITIO	DESMONTE	USO DE SUELO	
			1975-1977	1978-1981
RePriAg	R1-R5	Reciente	Vegetación Primaria	Agricultura
ReSecAg	L1-L6	Reciente	Vegetación Primaria	Agricultura
ReSecPa	P1-P6	Reciente	Vegetación Secundaria	Pastizal
AnPaAb	M1+P7	Antiguo	Pastizal inducido	Abandono
AnAgAb	H1-H2	Antiguo	Agricultura	Abandono

RESULTADOS Y DISCUSIÓN

I. FISONOMÍA

Las comunidades de vegetación secundaria en el área de estudio se pueden clasificar, considerando su fisonomía, en dos tipos principales: comunidades homogéneas con una sola especie dominante, y comunidades heterogéneas con dominancia de varias especies y varias formas de crecimiento.

1) Comunidades homogéneas con un dominante fisonómico.

Huizachales. Son comunidades simples en el sentido florístico y estructural, dominadas por *Acacia schaffneri* (Wats.) Herm. de forma arbustiva o arbórea arbustiva. En general son matorrales abiertos (30 a 60% de cobertura aérea) y de un solo estrato vertical, con escasa a nula cobertura subarbustiva y herbácea. Se presentan en áreas que han sido utilizadas durante largo tiempo para agricultura o para el establecimiento de pastizales inducidos, en los historiales AnAgAb (antiguos

campos agrícolas abandonados) y AnPaAb (antiguos pastizales abandonados), respectivamente.

Comunidades dominadas por otros árboles pequeños. Las comunidades dominadas por *Caesalpinia mexicana* A. Gray o por *Cordia boissieri* A. DC. presentan en ambos casos, una escasa cobertura herbácea y subarbustiva, posiblemente debido a la gran cantidad de hojarasca acumulada sobre el suelo en ambos tipos de comunidades. Las comunidades de *Caesalpinia mexicana* se registran para predios relacionados con un corto periodo de uso del suelo para agricultura después de desmontes recientes (historiales ReSecAg y RePriAg). Las comunidades de *Cordia boissieri* se registraron en sitios cuyo historial de uso de relaciona tanto con agricultura como con pastizales cultivados en predios recientemente desmontados. Aparentemente un factor determinante de la dominancia de *Cordia boissieri* es el suelo (generalmente más somero, más claro, y con pedregosidad).

Comunidades dominadas por una especie subarbustiva. Entre las comunidades de vegetación secundaria son comunes los escobillales puros o casi puros, en donde el dominante fisonómico es *Gymnosperma glutinosum* (Spreng.) Less. Existen escobillales de diferentes alturas; aparentemente la altura no está determinada por la edad de la comunidad sino por el tipo de suelo, ya que además de la altura, se observa diferencia en el vigor de las plantas. Los pobladores de la región coinciden en que este tipo de comunidad permanece durante mucho tiempo sin cambios en su composición. Otras comunidades secundarias de porte bajo en Linares, dominadas por una sola especie subarbustiva son las dominadas por *Solanum erianthum* D. Don.

2) Comunidades heterogéneas con más de un dominante fisonómico

Comunidades dominadas por arbustos multicaules y/o formas arbóreo-arbustivas. Existe una gran variedad de comunidades de vegetación secundaria en las cuales la fisonomía está dada por varias especies arbustivas y/o arbóreo-arbustivas. Entre las comunidades arbustivas son comunes aquellas en las que la dominancia fisonómica se reparte entre *Acacia rigidula* Benth. y todas o algunas de las siguientes especies: *Pithecellobium pallens* (Benth.) Standl., *Eysenhardtia polystachya* (Ortega) Sarg., *Zanthoxylum fagara* (L.) Sarg., *Diospyros texana* Scheele, *Celtis pallida* Torr., y *Acacia berlandieri* Benth. Entre las comunidades arbóreas se pueden mencionar aquéllas cuya fisonomía está dada por *Acacia farnesiana* (L.) Willd., *A. schaffneri*, *A. rigidula*, *Cordia boissieri*, y *Caesalpinia mexicana*, en diferentes combinaciones y proporciones.

Comunidades dominadas por varias especies de subarbustos. Son muy comunes entre los sitios con vegetación secundaria aquellos ocupados en su totalidad por una cobertura densa de dos o más especies subarbustivas como *Lantana velutina* Mart. & Gal., *Caesalpinia atropunctata* Eifert, *Dalea scandens* (Mill.) R.T. Clausen, *Meximalva filipes* (A. Gray) Fryx., y *Viguiera stenoloba* Blake en varias combinaciones y proporciones. Este tipo de comunidad se observó tanto en manchones de diferente tamaño dentro de los predios estudiados, como cubriendo prácticamente en su totalidad pequeñas parcelas con diferente tiempo de abandono.

Comunidades dominadas por una combinación de arbustos multicaules y una cubierta subarbustiva densa. Un tipo de comunidades parecidas a las anteriores son las que además de una cubierta subarbustiva densa incluyen una cobertura más o menos abierta de arbustos y/o pequeños árboles. Son comunes los sitios con una cobertura subarbustiva densa dominada por *Lantana velutina*, *Gymnosperma glutinosum*, *Eupatorium* spp., *Viguiera stenoloba*, *Herissantia crispa* (L.) Brizicky, y otras especies en diferentes combinaciones y proporciones; así como un estrato arbustivo y/o arbóreo-arbustivo (desde 10 hasta casi 90% cobertura) de especies como: *Acacia berlandieri*, *A. farnesiana*, *A. rigidula*, *Celtis pallida*, *Cordia boissieri*, *Diospyros texana*, *Pithecellobium pallens*, *Prosopis laevigata* (Willd.) M.C. Johnst., y *Zanthoxylum fagara*. Este tipo de comunidades se registró en los predios con historiales de uso RePriAg y ReSecAg, ambos relacionados con un corto período de agricultura de temporal después del desmonte y antes del abandono.

II. COMPOSICION FLORISTICA

Considerando el total de los muestreos se registran 64 especies de plantas leñosas (33 arbustivas y/o arbóreas, y 31 subarbustivas) pertenecientes a 30 familias (Tabla No. 2). La familia más importante entre las especies arbustivo - arbóreas es Leguminosae con 11 de las 33 especies (33%) y 1,458 de 2,725 individuos (53.5%). Las Leguminosas contribuyen con un 60.2% de la cobertura aérea total registrada. La gran importancia de esta familia en áreas con vegetación secundaria relativamente joven puede relacionarse con varios factores: escasa disponibilidad de nutrientes en el suelo, intolerancia a la sombra y mecanismos relacionados con la reproducción (dispersión, germinación, establecimiento, etc.).

La disponibilidad de nitrógeno en el suelo se relaciona íntimamente con el contenido total de materia orgánica y su reciclado (Woerner 1989). Los predios que han sido despojados de su cobertura vegetal natural y posteriormente sometidos a diversos usos agrícolas y pecuarios al ser abandonados es muy probable que presentan una baja disponibilidad de nitrógeno. Stevens & Walker (1970) mencionan que las especies de plantas capaces de fijar el nitrógeno atmosférico (característica común en las leguminosas), frecuentemente están presentes en las primeras fases de la sucesión.

La intolerancia a la sombra es otro factor que se relaciona con el establecimiento de las primeras especies de plantas en los predios abandonados. Bush & Van Auken (1986), mediante estudios de invernadero, determinaron que *Acacia smallii* Isely (= *A. farnesiana*) presenta la tasa más alta de crecimiento con la mayor exposición a la luz solar, y decrece a medida que la irradiación se reduce.

Flores (1993), en un estudio comparativo de la biología de establecimiento de plántulas de varias especies del matorral espinoso tamaulipeco, encontró que la mayoría de las leguminosas consideradas tuvieron una rápida velocidad de germinación en contraste con el resto de las especies.



Figura No. 1. Ubicación Geográfica del área de estudio

Después de Leguminosae, otras familias representadas en el estrato arbustivo - arbóreo de la vegetación secundaria estudiada, en orden decreciente de importancia por la cantidad de individuos presentes son: Boraginaceae, Ebenaceae, Euphorbiaceae, Rutaceae, Ulmaceae, y Rhamnaceae.

Las especies arbustivas y arbóreas con mayor densidad, cobertura, y frecuencia fueron: *Acacia rigidula*, *A. farnesiana*, y *Cordia boissieri*. Estas tres especies juntas, constituyen el 37.5% de la densidad y el 58.3% de la cobertura arbustivo - arbórea de los predios estudiados. Otras especies con alta densidad, cobertura y/o frecuencia fueron: *Caesalpinia mexicana*, *Pithecellobium pallens*, *Diospyros texana*, *Celtis pallida*, *Croton torreyanus* Muell.-Arg., *Zanthoxylum fagara*, *Eysenhardtia polystachya*, y *Karwinskia humboldtiana* (R. & S.) Zucc.

En el estrato subarbustivo, por la densidad y frecuencia de individuos, las familias más importantes son Verbenaceae, Compositae, y Euphorbiaceae, seguidas de Leguminosae y Malvaceae. Por cantidad de especies presentes, la familia más importante entre las subarbustivas es Compositae con 10 de las 31 especies, seguida de con 5 especies.

Los historiales de uso considerados reflejan una diferente composición florística y número de especies. Las áreas que fueron utilizadas por largo tiempo para agricultura y pastizales inducidos (desmontes antiguos) resultaron ser las más pobres en cuanto a composición (16 especies), mientras que las que fueron utilizadas por un periodo corto después del desmonte, poseen un mayor número de especies (33).

Las especies subarbustivas más importantes por su densidad y frecuencia fueron: *Lantana velutina*, *Gymnosperma glutinosum*, y *Croton cortesianus* H.B.K. Entre las tres, constituyen alrededor del 50% de individuos subarbustivos presentes en las parcelas de muestreo. Las especies subarbustivas que les siguen en importancia son: *Mimosa malacophylla* A. Gray, *Malpighia glabra* L., *Maximalva filipes*, *Dalea scandens*, *Viguiera stenoloba*, y *Caesalpinia atropunctata*. Por otra parte *Herissantia crispa*, *Malvastrum americanum* (L.) Torr., *Melochia pyramidata* L., *Eupatorium* sp., y otra especie de Compositae (Sp. 2), fueron importantes en un sitio del predio Rancherías y *Verbesina persicifolia* DC. fue importante en un sitio de El Puerto y en Los Hoyos.

La abundancia de *Gymnosperma glutinosum* en las áreas de estudio confirma que esta especie se correlaciona positivamente con el disturbio (Jurado 1986).

III. SIMILITUD FLORISTICA ENTRE SITIOS CON DIFERENTE HISTORIAL DE USO

Para analizar la semejanza florística entre las comunidades estudiadas se calcularon los índices de similitud de Jaccard (IS_j) y de Sorensen (IS_s). En la tabla No. 3 se resumen los resultados de los cálculos realizados considerando tres grupos de especies diferentes: total de especies muestreadas, especies arbustivas y arbóreas, y especies subarbustivas. Los resultados de ambos índices, indican una mayor similitud

florística entre los historiales RePriAg y ReSecAg (desmontes recientes, con uso agrícola durante corto tiempo) cuando se consideran todas las especies. Considerando únicamente el estrato subarbustivo, la mayor afinidad es entre ReSecAg (desmonte reciente, agricultura durante corto tiempo sobre predio con vegetación secundaria en 1975) y ReSecPa (desmonte reciente, para cultivo de pastizal durante corto tiempo) en el estrato subarbustivo. Sin embargo la mayor similitud florística se presentó entre los historiales RePriAg y ReSecPa cuando se consideran solamente las especies arbustivas y arbóreas.

El historial AnPaAb (praderas antiguas abandonadas), resulta ser el más disociado florísticamente, relacionándose, en todo caso con el AnAgAb (campo agrícola antiguo abandonado).

En términos generales existe una mayor similitud florística entre los predios con historiales RePriAg, ReSecAg, y ReSecPa, los cuales comparten la característica de haber tenido una cobertura vegetal (primaria o secundaria) hasta hace aproximadamente dos décadas en que fueron desmontados; mientras que en ese tiempo, los predios con historiales AnPaAb y AnAgAb (desmontes antiguos) ya se encontraban en uso agropecuario.

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Table No. 2. Especies registradas en la vegetación secundaria estudiada.

ARBUSTIVAS Y ARBOREAS ESPECIE	FAMILIA	SUBARBUSTIVAS ESPECIE	FAMILIA
<i>Acacia berlandieri</i>	Leguminosae	<i>Brickellia</i> sp.	Compositae
<i>Acacia farnesiana</i>	Leguminosae	<i>Caesalpinia atropunctata</i>	Leguminosae
<i>Acacia rigidula</i>	Leguminosae	<i>Calliandra eriophylla</i>	Leguminosae
<i>Acacia schaffneri</i>	Leguminosae	<i>Capsicum annum</i>	Solanaceae
<i>Bernardia myricaefolia</i>	Euphorbiaceae	<i>Croton ciliatoglandulifer</i>	Euphorbiaceae
<i>Bumelia celastrina</i>	Sapotaceae	<i>Croton cortesianus</i>	Euphorbiaceae
<i>Caesalpinia mexicana</i>	Leguminosae	<i>Dalea scandens</i>	Leguminosae
<i>Castela texana</i>	Simaroubaceae	<i>Desmanthus virgatus</i>	Leguminosae
<i>Celtis laevigata</i>	Ulmaceae	<i>Eupatorium cf. odoratum</i>	Compositae
<i>Celtis pallida</i>	Ulmaceae	<i>Eupatorium</i> sp.	Compositae
<i>Cercidium macrum</i>	Leguminosae	<i>Gymnosperma glutinosum</i>	Compositae
<i>Condalia hookeri</i>	Rhamnaceae	<i>Heimia salicifolia</i>	Lythraceae
<i>Cordia boissieri</i>	Boraginaceae	<i>Herissantia crispa</i>	Malvaceae
<i>Croton torreyanus</i>	Euphorbiaceae	<i>Krameria ramosissima</i>	Krameriaceae
<i>Diospyros texana</i>	Ebenaceae	<i>Lantana camara</i>	Verbenaceae
<i>Eysenhardtia polystachya</i>	Leguminosae	<i>Lantana</i> sp.	Verbenaceae
<i>Forestiera angustifolia</i>	Oleaceae	<i>Lantana velutina</i>	Verbenaceae
<i>Karwinskia humboldtiana</i>	Rhamnaceae	<i>Malpighia glabra</i>	Malpighiaceae
<i>Leucophyllum frutescens</i>	Scrophulariaceae	<i>Malvastrum americanum</i>	Malvaceae
<i>Mimosa monancistra</i>	Leguminosae	<i>Melochia pyramidata</i>	Sterculiaceae
<i>Opuntia lindheimeri</i>	Cactaceae	<i>Maximalva filipes</i>	Malvaceae
<i>Pithecellobium ebano</i>	Leguminosae	<i>Mimosa malacophylla</i>	Leguminosae
<i>Pithecellobium pallens</i>	Leguminosae	<i>Parthenium incanum</i>	Compositae
<i>Porlieria angustifolia</i>	Zygophyllaceae	<i>Parthenium lozanianum</i>	Compositae
<i>Prosopis laevigata</i>	Leguminosae	<i>Solanum erianthum</i>	Solanaceae
<i>Randia rhagocarpa</i>	Rubiaceae	Sp. 2	Fam. 2
<i>Salvia ballotaeflora</i>	Labiatae	Sp. 3	Fam. 3
<i>Schaefferia cuneifolia</i>	Celastraceae	<i>Turnera diffusa</i>	Turneraceae
Sp. 1	Fam. 1	<i>Verbesina persicifolia</i>	Compositae
<i>Xylosma flexuosa</i>	Flacourtiaceae	<i>Viguiera stenoloba</i>	Compositae
<i>Yucca filifera</i>	Agavaceae	<i>Zemisia hispida</i>	Compositae
<i>Zanthoxylum fagara</i>	Rutaceae		
<i>Ziziphus obtusifolia</i>	Rhamnaceae		

Tabla No. 3. Índices de similitud florística entre historiales de uso de suelo. Historial: RePriAg = Desmonte reciente de vegetación primaria para uso agrícola; ReSecAg = Desmonte reciente de vegetación secundaria para uso agrícola; ReSecPa = Desmonte reciente de vegetación secundaria para cultivo de pastizales; AnPaAb = Antiguo pastizal abandonado; y AnAgAb = Antiguo campo agrícola abandonado.

ÍNDICE DE JACCARD					ÍNDICE DE SORENSEN				
TOTAL DE ESPECIES MUESTREADAS									
HIST.	ReSecAg	ReSecPa	AnPaAb	AnAgAb	HIST.	ReSecAg	ReSecPa	AnPaAb	AnAgAb
RePriAg	63.33	58.93	30.77	40.82	RePriAg	77.55	73.33	47.06	57.97
ReSecAg		61.4	37.25	39.22	ReSecAg		76.09	54.29	56.34
ReSecPa			29.17	36.96	ReSecPa			45.16	53.97
AnPaAb				46.43	AnPaAb				63.41
ESPECIES ARBUSTIVAS Y ARBÓREAS									
HIST.	ReSecAg	ReSecPa	AnPaAb	AnAgAb	HIST.	ReSecAg	ReSecPa	AnPaAb	AnAgAb
RePriAg	66.67	77.78	32	52.17	RePriAg	80	87.5	48.48	68.57
ReSecAg		63.64	34.48	46.43	ReSecAg		77.78	51.28	63.41
ReSecPa			32.14	44.44	ReSecPa			48.65	61.54
AnPaAb				50	AnPaAb				66.67
ESPECIES SUBARBUSTIVAS									
HIST.	ReSecAg	ReSecPa	AnPaAb	AnAgAb	HIST.	ReSecAg	ReSecPa	AnPaAb	AnAgAb
RePriAg	60	44.83	29.63	30.77	RePriAg	75	61.9	45.71	47.06
ReSecAg		65.22	40.91	30.43	ReSecAg		78.95	58.06	46.67
ReSecPa			25	26.32	ReSecPa			40	41.67
AnPaAb				45.45	AnPaAb				58.82

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**ESTRUCTURA DE LA VEGETACION SECUNDARIA EN UN AREA DE
MATORRAL DEL NORESTE DE MEXICO**

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RESUMEN

Se describe la estructura cuantitativa de la vegetación secundaria de cinco áreas ubicadas al sur del municipio de Linares, Nuevo León, México (con clima, suelo y topografía similares, pero con historiales de uso de suelo diferentes). Los resultados muestran que las comunidades de vegetación secundaria en el área de estudio se caracterizan por la dominancia de pocas especies, entre las que destacan: *Acacia farnesiana*, *A. rigidula*, *Cordia boissieri*, *Caesalpinia mexicana*, y *Pithecellobium pallens*. Existe una gran variación en cuanto a densidad y cobertura totales (1,312 - 11,313 plantas/ha y 9-141% de cobertura aérea).

PALABRAS CLAVE: vegetación secundaria, estructura, matorral, Nuevo León, México

ABSTRACT

This paper deals with the quantitative structure of the secondary vegetation in five stands located in the southern part of Linares, México (with similar climate, soil and topography, but different land use history). Results show communities dominated by few species as *Acacia farnesiana*, *A. rigidula*, *Cordia boissieri*, *Caesalpinia mexicana*, and *Pithecellobium pallens*. Total density and cover varied significantly (1,312 - 11,313 plants/ha and 9% - 141%).

KEY WORDS: secondary vegetation, structure, thornscrub, Nuevo León, México

INTRODUCCION

La cubierta vegetal del municipio de Linares se ha convertido en un complejo mosaico que incluye áreas de uso agropecuario, fragmentos de vegetación primaria con grado alto de disturbio, y numerosas fragmentos de vegetación secundaria de diferentes dimensiones y edades. Para 1986 más del 50% del territorio municipal había sufrido cambios radicales de uso se suelo (Treviño 1992, 1996).

Este artículo sobre estructura cuantitativa es el segundo de una serie en la que se pretende dar a conocer los resultados del análisis de la vegetación secundaria de Linares, Nuevo León, México, realizado como trabajo de tesis de maestría de la primera autora (González 1996).

AREA DE ESTUDIO Y METODOLOGIA

El área de estudio y la metodología para recabar los datos de campo para este estudio son los mismos que se describen en González *et al.* (1998). Se realizaron muestreos de vegetación en 21 sitios ubicados al sur del municipio de Linares, Nuevo León, México. Dichos sitios comparten características físicas similares (clima, suelo, y topografía) y difieren en su historial de uso de suelo, el cual para este trabajo se clasificó en 5 tipos: Sitios cuya vegetación primaria fue eliminada hace menos de 20 años para utilizarse temporalmente para agricultura (RePriAg); sitios cuya vegetación secundaria fue nuevamente eliminada hace menos de 20 años para utilizarse temporalmente para agricultura (ReSecAg); sitios cuya vegetación secundaria fue nuevamente eliminada hace menos de 20 años para establecimiento temporal de pastizales (ReSecPa); sitios que fueron desmontados hace más de 25 años, utilizados temporalmente como pastizal y abandonados desde hace por lo menos 18 años (AnPaAb); y sitios que fueron desmontados hace más de 25 años, utilizados temporalmente para agricultura y abandonados desde hace por lo menos 18 años (AnAgAb).

Un primer análisis se realizó con los datos de los 21 sitios de vegetación secundaria muestreados en su conjunto. Se obtuvieron los parámetros estructurales básicos: densidad, cobertura y frecuencia por especie, así como sus valores relativos. Para evaluar la importancia relativa de las diversas especies se obtuvo el índice de valor de importancia de Curtis (1959) sumando los tres valores relativos. Un segundo análisis se realizó con los datos de cada historial de uso por separado; en este caso no se consideran valores de frecuencia dado el reducido número de parcelas por historial. Así mismo, se obtuvieron los datos de densidad total y cobertura total por parcela de muestreo y por historial de uso de suelo.

RESULTADOS Y DISCUSION

En la tabla No. 1 se resumen los parámetros estructurales que caracterizan a las comunidades de vegetación secundaria estudiadas en su conjunto. La figura No. 1, ilustra los valores de importancia de las principales especies. Las especies más importantes en la vegetación secundaria estudiada son *Acacia rigidula* Benth., *A. farnesiana* (L.) Willd., y *Cordia boissieri* A.DC. De éstas, la segunda es la especie reportada más frecuentemente como invasora de pastizales y como una de las primeras especies en establecerse en campos de cultivo en desuso (Peñaloza & Reid 1989; Bush & Van Auken 1986, 1987), mientras que *Acacia rigidula* y *Cordia boissieri*, junto con *Pithecellobium pallens* (Benth.) Standl., especies que sigue en valor de importancia, fueron registradas por Jurado (1986) como especies con amplio espectro de tolerancia a factores físicos.

En la figura No. 1 se destaca también que las tres variables involucradas en el valor de importancia: densidad relativa, cobertura relativa y frecuencia relativa, contribuyen en diferente proporción a dicho valor. *Acacia rigidula*, por ejemplo, es la especie más importante debido a su mayor densidad, ya que en cuanto a cobertura y frecuencia comparte valores similares a los de *A. farnesiana* y *Cordia boissieri*, que le siguen en importancia. *Caesalpinia mexicana* A. Gray, por otra parte, tiene una densidad relativa muy parecida a la de *Cordia boissieri*, pero su valor de importancia es mucho menor debido a su baja cobertura y frecuencia. *Pithecellobium pallens* y *Diospyros texana* Scheele comparten el mismo valor de frecuencia y similar densidad, sin embargo difieren considerablemente en cuanto a cobertura, resultando un mayor valor de importancia para el primero.

En la Table No. 2 se resumen los parámetros estructurales de las principales especies que caracterizan a las comunidades de los diferentes historiales de uso considerados y se presentan los datos de porcentaje de cobertura y densidad total (ind./ha) para cada tipo de historial.

En el historial RePriAg (desmonte reciente de predio con vegetación primaria para uso agrícola), *Caesalpinia mexicana* es la especie más importante (25.85%). Presenta aproximadamente la misma cobertura que *Acacia farnesiana*, sin embargo su densidad es mucho más alta y está dada por un gran número de individuos juveniles.

En el historial ReSecAg (desmonte reciente en predio con vegetación secundaria para uso agrícola), la especie más importante es *Acacia rigidula* (31.5%); le sigue *Diospyros texana*, que a diferencia de su comportamiento en los demás predios, en este alcanza el segundo valor de importancia (11.8%) debido a su densidad, ya que por lo menos *A. farnesiana*, *Caesalpinia mexicana*, *A. berlandieri* Benth., y *Celtis pallida* Torr., tienen una mayor cobertura. Es decir, existen una gran cantidad de individuos de pequeña talla de *Diospyros* (cobertura de 0.75 m²/individuo) y pocos individuos grandes (2.5 a 5.5 m²/individuo) de las tres especies con las que se compara. *Croton torreyanus* Muell.-Arg., ocupa el tercer lugar en valor de importancia en este predio; al igual que *D. texana*, alcanza dicho valor por su densidad, ya que su cobertura es mucho menor que la de varias especies con valores de importancia menores.

Tabla No. 1. Valores relativos y valores de importancia (en orden de mayor a menor) para las especies arbustivas y arbóreas presentes en los predios con vegetación secundaria estudiados.

ESPECIE	Dens. rel. (%)	Cob. rel. (%)	Frec. rel. (%)	Valor importancia
<i>Acacia rigidula</i>	17.17	20.69	8.58	46.44
<i>Acacia farnesiana</i>	10.50	18.33	9.07	37.90
<i>Cordia boissieri</i>	9.83	19.32	7.84	37.00
<i>Pithecellobium pallens</i>	7.16	6.66	6.62	20.44
<i>Caesalpinia mexicana</i>	9.25	5.86	2.21	17.31
<i>Zanthoxylum fagara</i>	5.14	4.21	6.86	16.22
<i>Diospyros texana</i>	6.42	2.37	6.62	15.41
<i>Celtis pallida</i>	3.19	4.37	6.86	14.43
<i>Eysenhardtia polystachya</i>	4.99	2.50	3.43	10.92
<i>Croton torreyanus</i>	6.17	0.91	3.19	10.26
<i>Karwinskia humboldtiana</i>	2.31	0.88	5.15	8.34
<i>Prosopis laevigata</i>	2.06	1.61	3.92	7.58
<i>Opuntia lindheimeri</i>	2.17	1.20	3.92	7.29
<i>Randia rhagocarpa</i>	2.13	0.58	3.68	6.39
<i>Acacia berlandieri</i>	0.99	2.40	2.21	5.59
<i>Burmelia celastrina</i>	1.83	1.16	2.45	5.45
<i>Salvia ballotaeiflora</i>	2.50	0.56	2.21	5.26
<i>Forestiera angustifolia</i>	1.17	0.81	2.94	4.93
<i>Ziziphus obtusifolia</i>	0.59	0.71	1.47	2.77
<i>Cercidium macrum</i>	0.18	1.22	1.23	2.63
<i>Condalia hookeri</i>	0.77	0.58	1.23	2.58
<i>Leucophyllum frutescens</i>	0.70	0.73	0.74	2.16
<i>Porlieria angustifolia</i>	0.29	0.11	1.72	2.12
<i>Celtis laevigata</i>	0.73	0.22	0.98	1.94
<i>Mimosa monancistra</i>	0.66	0.43	0.74	1.83
<i>Pithecellobium ebano</i>	0.33	0.52	0.98	1.83
<i>Acacia schaffneri</i>	0.22	0.54	0.98	1.74
<i>Castela texana</i>	0.26	0.41	0.25	0.91
<i>Schaefferia cuneifolia</i>	0.11	0.02	0.74	0.86
<i>Bernardia myricaefolia</i>	0.07	0.01	0.49	0.58
<i>Xylosma flexuosa</i>	0.04	0.05	0.25	0.33
<i>Yucca filifera</i>	0.04	0.01	0.25	0.29
<i>Zanthoxylum fagara</i>	0.04	0.00	0.25	0.29
TOTAL	100	100	100	300

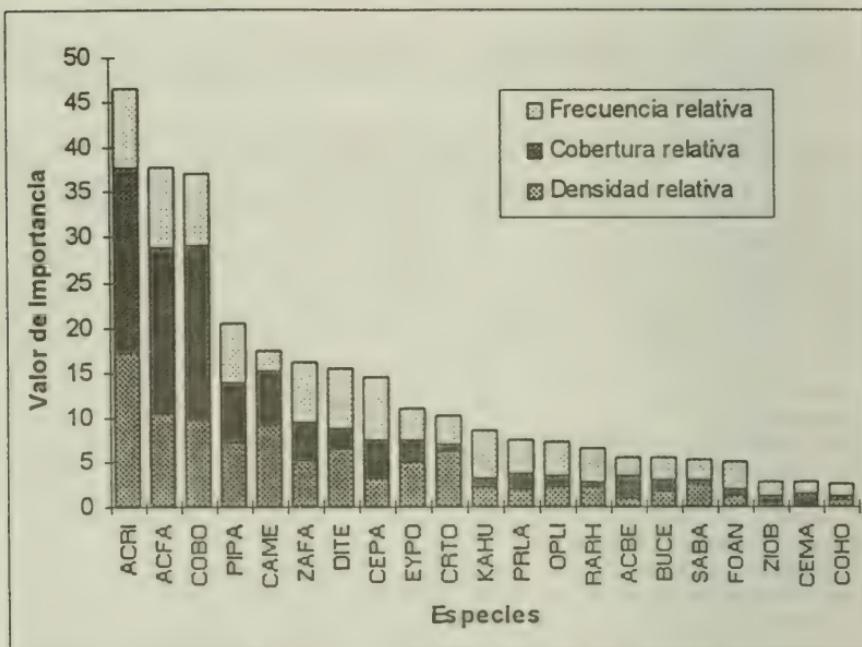


Figura No. 1. Valor de importancia y parámetros estructurales de las principales 21 especies arbustivas u arbóreas muestreadas (Los nombres completos de las especies aparecen en la table No. 1).

En el predio con historial ReSecPa (desmonte reciente de vegetación secundaria para cultivo de pastos), la especie con el mayor valor de importancia (25%) resultó ser *Cordia boissieri*, que presenta un valor muy alto de cobertura (34%); *Acacia rigidula* le sigue en importancia con un valor de densidad bastante más alto pero con mucha menor cobertura. Siguen en importancia *Pithecellobium pallens* por cobertura, y *Zanthoxylum fagara* (L.) Sarg. por densidad. Los lugares 5 y 6 en valor de importancia corresponden a *Eysenhardtia polystachya* (Ortega) Sarg. y *A. farnesiana*, que tiene mucha menor densidad, pero mayor cobertura, en comparación de las especies que le siguen en importancia.

Tabla No. 2. Especies arbustivas y arbóreas con valores de importancia (densidad + cobertura) mas altos en cada uno de los historiales de uso considerados: RePriAg (desmonte reciente de vegetación primaria para uso agrícola); ReSecAg (desmonte reciente de vegetación secundaria para uso agrícola); ReSecPa (desmonte reciente de vegetación secundaria para cultivo de pastizal); AnPaAb (antiguo pastizal abandonado) y AnAgAb (antiguo campo agrícola abandonado).

Historiales de uso y Especies principales	Dens. rel. (%)	Cob. rel. (%)	Valor Imp. (%)	Dens. (Ind./ Ha)	Cob./Ha (m ²)
RePriAg:					
<i>Caesalpinia mexicana</i>	33.60	18.10	25.85	1318.75	1163.85
<i>Pithecellobium pallens</i>	13.69	11.34	12.52	537.50	729.09
<i>Acacia farnesiana</i>	6.53	18.38	12.45	256.25	1181.86
<i>Cordia boissieri</i>	6.69	16.98	11.84	262.50	1092.01
<i>Acacia rigidula</i>	6.21	13.68	9.94	243.75	879.39
<i>Eysenhardtia polystachya</i>	8.60	3.26	5.93	337.50	209.66
Cobertura total por historial					64.30%
ReSecAg:					
<i>Acacia rigidula</i>	26.68	36.37	31.52	911.46	2433.57
<i>Diospyros texana</i>	17.07	6.53	11.80	583.33	437.20
<i>Croton torreyanus</i>	14.48	2.16	8.32	494.79	144.45
<i>Acacia farnesiana</i>	4.12	9.94	7.03	140.63	664.83
<i>Caesalpinia mexicana</i>	6.25	7.79	7.02	213.54	521.54
<i>Acacia berlandieri</i>	3.20	9.06	6.13	109.38	605.93
Cobertura total por historial					66.91%
ReSecPa:					
<i>Cordia boissieri</i>	16.90	34.01	25.45	942.71	3361.61
<i>Acacia rigidula</i>	23.25	20.57	21.91	1296.88	2033.42
<i>Pithecellobium pallens</i>	7.56	8.14	7.85	421.88	805.08
<i>Zanthoxylum fagara</i>	8.50	5.98	7.24	473.96	591.39
<i>Eysenhardtia polystachya</i>	7.38	4.51	5.94	411.46	445.98
<i>Acacia farnesiana</i>	3.55	7.82	5.69	197.92	773.40
Cobertura total por historial					98.85%
AnPaAb					
<i>Acacia farnesiana</i>	36.36	58.56	47.46	687.50	3418.02
<i>Cordia boissieri</i>	22.31	23.82	23.07	421.88	1390.29
<i>Mimosa monancistra</i>	14.05	5.46	9.76	265.63	318.96
<i>Prosopis laevigata</i>	14.05	4.35	9.20	265.63	254.12
<i>Pithecellobium pallens</i>	3.31	4.33	3.82	62.50	252.77
<i>Forestiera angustifolia</i>	3.31	0.84	2.07	62.50	49.24
Cobertura total por historial					58.37%
AnAgAb					
<i>Acacia farnesiana</i>	55.06	69.72	62.39	2125.00	3318.01
<i>Forestiera angustifolia</i>	6.88	8.81	7.85	265.63	419.31
<i>Pithecellobium pallens</i>	8.10	7.22	7.66	312.50	343.74
<i>Prosopis laevigata</i>	10.53	3.60	7.06	406.25	171.41
<i>Zanthoxylum fagara</i>	6.88	2.57	4.73	265.63	122.19
<i>Karwinskia humboldtiana</i>	4.45	2.50	3.48	171.88	118.82
Cobertura total por historial					47.59%

En los sitios con historial AnPaAb (antiguo pastizal inducido en desuso), *Acacia farnesiana* ocupa el primer lugar en importancia (47%) con el 36.4% de la densidad

total, y el 58.5% de la cobertura total. La segunda especie, también con un valor alto de importancia (casi el 25%), es *Cordia boissieri*; le siguen, con valores mucho menores *Mimosa monancistra* Benth. y *Prosopis laevigata* (Willd.) M.C. Johnst., este último con la misma cobertura pero bastante mayor densidad que *Pithecellobium pallens*, que presenta un valor de importancia mucho menor.

En el historial AnAgAb (antiguo campo de cultivo en desuso), la especie dominante (valor de importancia = 62%) es también *Acacia farnesiana* con el 55% de la densidad total y casi el 70% de la cobertura total. Las especies que le siguen, con mucha menor importancia son: *Forestiera angustifolia* Torr., *Pithecellobium pallens*, *Prosopis laevigata*, y *Zanthoxylum fagara*.

Si se comparan los valores de importancia registrados en este trabajo sobre vegetación secundaria, con los obtenidos por Heiseke & Foroughbakhch (1985), se observa que ninguna de las tres especies con los mayores valores de importancia en este estudio (*Acacia rigidula*, *A. farnesiana*, y *Cordia boissieri*), se cuenta entre las especies con los mayores valores de importancia registrados por los autores mencionados. En ese trabajo aparecen como especies más importantes algunas de las que aquí presentan importancia secundaria: *Diospyros texana*, *Pithecellobium pallens*, y *Zanthoxylum fagara*; además de algunas de importancia mucho menor en la vegetación secundaria estudiada, como *Forestiera angustifolia*, *Condalia hookeri* M.C. Johnst., y *Bernardia myricaefolia* (Scheele) Wats. Esto podría indicar que las especies antes mencionadas reemplazan (total o casi totalmente como en el caso del huizache, o por lo menos en importancia relativa) a las especies que ocupan los primeros lugares durante las fases tempranas de desarrollo de los estratos leñosos del matorral.

Otro rasgo comparativo que podría apoyar esta hipótesis es la ausencia de *Acacia farnesiana* tanto en el matorral alto (sin disturbio aparente) como el matorral bajo estudiados por Rodríguez (1994), así como la frecuencia y densidad mínimas registradas por el mismo autor para *Cordia boissieri*, lo que podría indicar el reemplazo de estas especies en matorrales más desarrollados.

Tanto en los resultados de Heiseke & Foroughbakhch (1985) como en los de Rodríguez (1994) para el matorral alto sin disturbio, los mayores valores de densidad corresponden a especies que en la vegetación secundaria aquí estudiada, ocupan valores intermedios de importancia como *Diospyros texana*, *Pithecellobium pallens*, y *Celtis pallida*; o valores bajos como *Condalia hookeri*, *Bumelia celastrina* H.B.K., *Pithecellobium ebano* (Berland.) C.H. Mull., *Ziziphus obtusifolia* (Torr. & Gray) A. Gray, y *Xylosoma flexuosa* (H.B.K.) O. Ktze., o aún más,^a a especies que no se registraron en la vegetación secundaria, como *Amyris texana* (Buckl.) P. Wils.

En cuanto a los valores totales de cobertura o porcentaje de superficie ocupada por las proyecciones verticales de las copas, en la Tabla No. 2 se muestra que el historial ReSecPa (desmonte reciente de vegetación secundaria para establecimiento de pastizales), tiene el mayor valor (98.8%); sin embargo en la Tabla No. 3 se observa que el porcentaje de cobertura en las parcelas correspondientes (P1 a P6) se extiende en un rango desde 43.81% hasta 141.32%. Le sigue el historial ReSecAg (desmonte reciente de vegetación secundaria para uso agrícola) con 66.9% de cobertura en conjunto, pero con áreas muy abiertas de solamente 9.08% de cobertura arbustiva y arbórea, y áreas en donde las copas se sobreponen con 116.93% de cobertura (sitios L1 a L6). El historial RePriAg (desmonte reciente de vegetación primaria para uso

agrícola) tiene una cobertura aérea muy similar al ReSecAg (desmonte reciente de vegetación secundaria para uso agrícola) de 64.3%, sin embargo en este caso el rango entre parcelas (R1 a R5) es menos amplio y va de 27.65% en la parcela con matorral más abierto hasta 100.31% en la parcela con matorral más cerrado.

Tabla No. 3. Densidad y cobertura del total de especies arbustivas y arbóreas por sitio de muestreo.

SITIO	Parcela A		Parcela B	
	ind/ha	%COB	ind/ha	%COB
H1	4062.5	60.22	2312.5	32.64
H2	3750.0	49.57	5312.5	47.93
L1	4125.0	82.33	4000.0	88.53
L2	2125.0	25.71	1312.5	17.41
L3	2625.0	9.08	3000.0	66.16
L4	6437.5	91.37	3937.5	87.03
L5	4687.5	116.93	4062.5	109.45
L6	2125.0	41.99	2562.5	66.93
M1	1750.0	38.15	2750.0	33.23
P1	6062.5	93.54	6312.5	122.43
P2	3187.5	71.70	5500.0	109.30
P3	10187.5	141.32	11312.5	134.58
P4	3625.0	63.56	2750.0	89.81
P5	5937.5	106.84	4625.0	121.51
P6	4062.5	87.78	3437.5	43.81
P7	1312.5	95.88	1750.0	66.23
R1	2687.5	49.88	3812.5	96.17
R2	4750.0	33.26	2187.5	27.65
R3	2562.5	57.30	3125.0	81.50
R4	3875.0	61.19	4250.0	62.41
R5	6500.0	73.34	5562.5	100.31

Los historiales con menor porcentaje de cobertura aérea son el AnPaAb (antiguos pastizales inducidos en desuso) con 58.3% de cobertura, y el AnAgAb (antiguos terrenos agrícolas en desuso) con 47.5% de cobertura en conjunto, que varían entre 33 a 60% (sitios H1 y H2). Cabe hacer notar que el historial AnPaAb incluye dos sitios en dos predios diferentes (M1 y P7) y con fisonomías, coberturas y densidades disímiles. Se agruparon en este trabajo debido a que ambos aparecen en la carta de uso de suelo de 1975 como pastizales inducidos.

Los valores de densidad total (individuos/ha) de mayor a menor son 5578 en el historial ReSecPa (desmonte reciente de vegetación secundaria para cultivo de pastos); 3925 en el historial RePriAg (desmonte reciente de vegetación primaria para uso

agrícola); 3859 en el historial AnAgAb (campo de cultivo en desuso); 3416 en el historial ReSecAg (desmonte reciente de vegetación secundaria para uso agrícola); y 1890 en el historial AnPaAb (antiguos pastizales inducidos en desuso). En este apartado resulta interesante hacer notar la baja cobertura en los sitios con historial AnAgAb (antiguo campo agrícola abandonado), a pesar de su alta densidad. Al igual que los valores de cobertura, los valores de densidad varían ampliamente entre las parcelas de un mismo historial.

Los resultados de este trabajo indican un amplio rango de densidad y cobertura totales por parcela de muestreo dentro de cada historial de uso considerado. Las especies más importantes en cada historial también difieren aunque de una forma menos notoria. Dicha variación sugiere que la clasificación de los sitios de muestreo, por historial de uso de suelo que se consideró en este trabajo no refleja diferencias en cuanto a la estructura de la vegetación.

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DIVERSIDAD FLORISTICA DE LA VEGETACION SECUNDARIA EN UN AREA DE MATORRAL DEL NORESTE DE MEXICO

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RESUMEN

Se compara la diversidad florística de cinco áreas ubicadas en el sur del municipio de Linares, Nuevo León, México, ocupadas por vegetación secundaria de menos de 20 años de desarrollo que comparten similares condiciones físicas (clima, suelo, y topografía) y difieren en su historial de uso de suelo. Los resultados revelan una menor diversidad en los predios relacionados con períodos más largos de aprovechamiento agropecuario, en comparación con los predios que después del desmonte fueron utilizados durante pocos años.

PALABRAS CLAVE: vegetación secundaria, diversidad florística, matorral, Nuevo León, México

ABSTRACT'

This study deals with floristic diversity in five secondary vegetation stands, less than 20 years old, located in the southern part of Linares, México (with similar climate, soil and topography, but different land use history). Sites that were utilized for a long time showed less richness and diversity than sites utilized for a short time after clearing.

KEY WORDS: secondary vegetation, floristic diversity, thornscrub, Nuevo León, México

INTRODUCCION

Los efectos adversos del estrés pueden reflejarse en una reducción de la diversidad o en un cambio en la forma de la distribución de abundancias de las especies (Magurran 1988). La misma autora sugiere que la diversidad se puede manejar como un índice del "bienestar" del ecosistema, aunque advierte que juicios basados únicamente en índices de diversidad, sin considerar otra información ecológica, pueden llevar a conclusiones erróneas; menciona, además, que el incremento en diversidad puede también ser el costo de un cambio en la composición de la comunidad.

En el área de Linares, Nuevo León recientemente se han realizado estudios de diversidad florística considerando factores de disturbio y fragmentación de hábitats: Rodríguez (1994) realizó diversos análisis de fitodiversidad, comparando una comunidad de matorral no perturbada (Matorral alto) con una perturbada (Matorral bajo). Medina Cortés (1995), determinó mediante los índices de Shannon & Wiener, y de Simpson, la fitodiversidad presente en fragmentos de vegetación de dos diferentes tamaños (>100 ha y <10 ha) y de por lo menos 20 años de desarrollo. Con el propósito de continuar con esta línea de investigación, en este trabajo se comparan la riqueza y la diversidad florística de predios con vegetación secundaria que difieren en su historial de uso.

AREA DE ESTUDIO Y METODOLOGIA

El área de estudio y la metodología para recabar los datos de campo son los mismos que se describen en González *et al.* (1998). Se realizaron muestreos de vegetación en 21 sitios ubicados al sur del municipio de Linares, Nuevo León, México. Dichos sitios comparten características físicas similares (clima, suelo, y topografía) y difieren en su historial de uso de suelo, el cual para este trabajo se clasificó en 5 tipos: Sitios cuya vegetación primaria fue eliminada hace menos de 20 años para utilizarse temporalmente para agricultura (RePriAg); sitios cuya vegetación secundaria fue nuevamente eliminada hace menos de 20 años para utilizarse temporalmente para agricultura (ReSecAg); sitios cuya vegetación secundaria fue eliminada hace menos de 20 años para establecimiento temporal de pastizales (ReSecPa); sitios que fueron desmontados hace mas de 25 años, utilizados temporalmente como pastizal y abandonados desde hace por lo menos 18 años (AnPaAb); y sitios que fueron desmontados hace mas de 25 años, utilizados temporalmente para agricultura y abandonados desde hace por lo menos 18 años (AnAgAb).

En el presente estudio se obtuvieron, para cada parcela de muestreo, el índice de riqueza de Margalef (DMg) y dos índices de heterogeneidad; el índice de Simpson (D), que es una medida de dominancia, y el índice de Shannon (H) que refleja mejor la diversidad de poblaciones ricas florísticamente.

La estimación de los índices antes mencionados se obtuvo mediante las siguientes relaciones: $DMg = S-1)/\ln N$; $D = \sum (pi)^2$; $H = -\sum [pi (\ln pi)]$. Donde pi representa la relación ni/N , cuando N representa algún valor de importancia (en este caso densidad absoluta), ni es el valor de importancia para cada componente (en este caso especies), y S es el número de especies.

La aplicación de D y de H permite comparar sus resultados. Para ello se obtuvo el complemento del índice de Simpson ($1 - D$) y el índice de Shannon se ajustó a una escala de 0 a 1 mediante la fórmula $H/\ln(S)$, también conocida como índice de equitatividad (E). De esta manera, ambos índices reflejan la diversidad (heterogeneidad) en una escala de 0 a 1, en donde los valores cercanos a 0 indican muy poca diversidad y los valores cercanos a 1 denotan gran diversidad.

RESULTADOS Y DISCUSIÓN

Se determinaron tres valores para cada índice: el primero considera todas las especies, el segundo incluye únicamente las especies arbustivas y arbóreas, el tercero toma en cuenta únicamente las especies subarbustivas (Tabla No. 1).

Para realizar el análisis de la diversidad de las comunidades con diferentes historiales de uso de suelo, se graficaron los valores medios y las desviaciones estándar de el índice de Equitatividad de Shannon (E) y del complemento del índice de Simpson ($1 - D$) (Figura No. 1).

Un análisis preliminar de los datos indica cierta diferencia entre los valores obtenidos para los historiales RePriAg, ReSecAg, y ReSecPa por un lado, y los historiales AnPaAb y AnAgAb por otro lado (Tabla No. 1), siendo más alta la diversidad y la riqueza en los primeros que en los segundos. Es decir, los predios que presentaban vegetación natural (primaria o secundaria) entre 1975 y 1977; y que posteriormente fueron desmontados, brevemente utilizados y después abandonados, presentan actualmente una cubierta vegetal con mayor diversidad (menor dominancia específica) y mayor riqueza, en relación a los predios que en 1975-1977, y durante tiempo no definido anteriormente, estaban ocupados por pastizales inducidos y por agricultura, y que posteriormente fueron abandonados.

Al comparar E , medida que considera el número de especies ($E = H/\ln S$, complemento del índice de Shannon cargado a favor de especies raras), con $1 - D$ (complemento del índice de Simpson cargado a favor de las especies comunes o dominantes), se observa que la tendencia de uno y otro índice no es la misma, lo que sugiere que existen diferencias en cuanto al peso de la dominancia y la equitatividad que determinan la diversidad de los predios. En el predio AnPaAb, por ejemplo, la diversidad ($1 - D$) es ligeramente menor en comparación con los tres tipos de historial con desmonte reciente, sin embargo su valor de equitatividad (E) es mayor que en éstos.

Los valores calculados para el índice de Simpson sugieren que la dominancia de una o pocas especies está relacionada directamente con el tipo de historial de uso de

suelo. Los valores de diversidad (1 - D) más bajos se presentan en los predios cuyo historial de uso implica mayor disturbio.

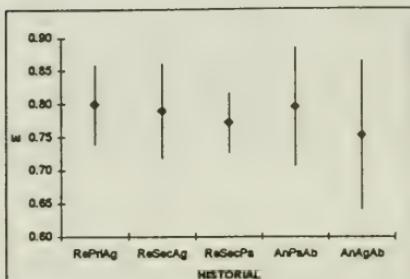
Tabla No. 1. Índices de diversidad por historial: E = índice de equitatividad de Shannon; 1 - D = complemento del índice de Simpson (diversidad) y DMg = índice de riqueza de Margalef. Historial: RePriAg = Desmonte reciente de vegetación primaria para uso agrícola; ReSecAg = Desmonte reciente de vegetación secundaria para uso agrícola; ReSecPa = Desmonte reciente de vegetación secundaria para cultivo de pastizales; AnPaAb = Antiguo pastizal abandonado; y AnAgAb = Antiguo campo agrícola abandonado.

INDICE:	HISTORIAL				
	RePriAg	ReSecAg	ReSecPa	AnPaAb	AnAgAb
TOTAL DE ESPECIES MUESTREADAS					
E	0.80	0.79	0.77	0.80	0.75
1 - D	0.85	0.84	0.85	0.80	0.74
DMg	3.66	3.45	3.39	2.26	2.13
ESPECIES ARBUSTIVO-ARBOREAS					
E	0.75	0.76	0.79	0.73	0.55
1 - D	0.72	0.74	0.79	0.62	0.49
DMg	2.43	2.22	2.41	1.39	1.33
ESPECIES SUBARBUSTIVAS					
E	0.76	0.76	0.70	0.85	0.72
1 - D	0.72	0.71	0.67	0.66	0.60
DMg	1.80	1.61	1.35	1.05	0.97

Los valores calculados para E (equitatividad), indican que el historial AnAgAb (antiguo terreno agrícola en desuso) es, en términos generales, el menos equitativo, mientras que el tipo de historial con mayor equitatividad en cuanto a subarbustivas es el AnPaAb (antiguo pastizal inducido en desuso). En cuanto a arbustivas y arbóreas el historial más equitativo es el ReSecPa (desmonte reciente de vegetación secundaria para cultivo de pastizal).

La amplia desviación estándar de los valores de equitatividad (E) y diversidad (1 - D), que se observa en el caso del historial AnAgAb se debe a que las parcelas muestreadas representan dos tipos de campos de cultivo abandonados: áreas que albergaron cultivos anuales, y huertas de frutales; en las primeras la diversidad es muy baja, mientras que en las segundas, alcanza valores similares a los de los históricos que involucran menor disturbio.

INDICE DE EQUITATIVIDAD DE SHANNON



INDICE DE DIVERSIDAD DE SIMPSON

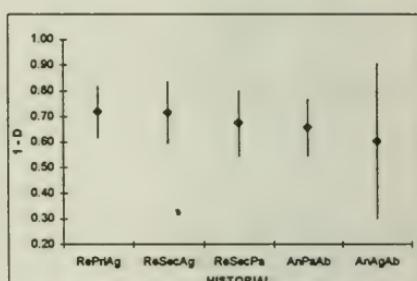
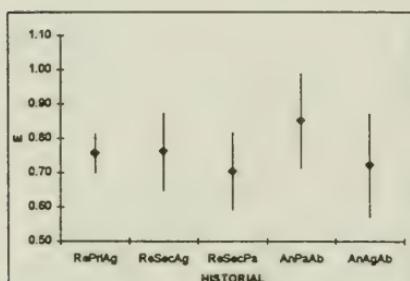
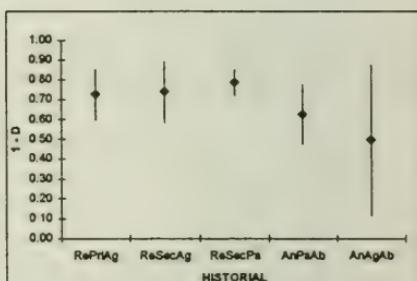
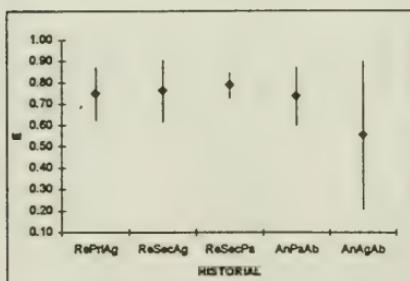
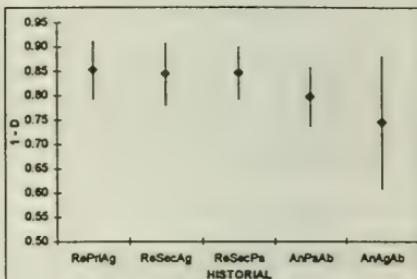


Figura No. 1. Media \pm 1 desviación estándar de el Indice de equitatividad de Shannon (E) y del Indice de diversidad de Simpson (1 - D), para los 5 tipos de historiales de uso de suelo reconocidos. A) total de especies; B) especies arbustivas y arbóreas; y C) especies subarbustivas.

La clasificación de las parcelas de muestreo, por historial de uso de suelo que se consideró en este trabajo, parece no reflejar diferencias en cuanto a la estructura de la vegetación (González *et al.* 1998); sin embargo, sí refleja diferencias muy obvias en cuanto a riqueza florística se refiere, siendo los historiales que involucran desmontes recientes (menos de 20 años) y períodos cortos de cambio de uso de suelo, más ricos en comparación con los desmontes antiguos y períodos largos de utilización del suelo con fines agrícolas o ganaderos.

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THE SUBALPINE AND ALPINE VASCULAR FLORA OF THE NEOTA WILDERNESS AREA IN THE NORTHERN NEVER SUMMER RANGE OF NORTH-CENTRAL COLORADO

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ABSTRACT

The vascular flora of the Neota Wilderness Area in the northern Never Summer Range of Colorado was inventoried during 1992 and 1993. Approximately 40 km², the area contained both subalpine and alpine vegetation. A subalpine/alpine flora of 54 families, 169 genera, and 301 species, with a predominately boreal-montane, western North American distribution is documented. An alpine flora of 39 families, 118 genera, and 203 species, with a predominately alpine, western North American distribution is reported. *Subularia aquatica* L. is reported as a new record for the state flora of Colorado.

KEY WORDS: Neota Wilderness, flora, Colorado, subalpine, alpine, phytogeography, *Subularia aquatica*

INTRODUCTION

The Neota Wilderness is located in the southern Rocky Mountains in north-central Colorado between Cameron Pass and the northwest boundary of Rocky Mountain National Park. It is a relatively small wilderness area, only 40 km² (USDA Forest Service 1984), and was designated wilderness status in 1980 as part of the Colorado Wilderness Act. It is located at approximately 40° 32' N latitude and 105° 50' W longitude.

Wilderness areas in Colorado have received little floristic attention from investigators as most floristic work has been focused on entire mountain ranges or regions of the state (Hartman & Rottman 1985a, 1985b, 1985c, 1987, 1988; Vanderhorst 1992; Kastning 1990; Weber 1976, 1987, 1990). Two wilderness areas which have been floristically studied in recent years are the Indian Peaks Wilderness

(Komarkova 1979) and the Eagles Nest Wilderness Area (Hogan 1992). Except for these studies, little specific floristic information has been collected for each wilderness area.

This study was conducted during the summers of 1992 and 1993 to inventory and provide a checklist of the subalpine and alpine vascular flora of the Neota Wilderness. Additional objectives included floristic and phytogeographic comparisons of the Neota Wilderness flora with that of other subalpine and alpine floras in Colorado (Nelson 1993).

SITE

Geology. The dominating topographic feature of the Neota Wilderness is Iron Mountain (3738 m), the summit of which lies just outside the western boundary of the wilderness. Three major ridges extend from the summit of Iron Mountain to the north and north-east and form most of the high alpine zone as well as the box canyons in the subalpine zone. Several small subparallel streams drain the area through steepwalled, glaciated valleys and flow generally east-northeast into tributary streams to the Cache La Poudre River. The ridges that separate the streams are generally flat-topped and slope gently to the northeast. Elevations within the wilderness range from approximately 3019 m near the northern boundary to 3667 m near the summit of Iron Mountain. Other peaks within the wilderness include Flattop Mountain (3461 m), Mount Neota (3577 m), Thunder Mountain (3672 m), and Bald Mountain (3292 m).

The Neota Wilderness is underlain by the Precambrian core (schists and gneisses) of the Front Range of Colorado (Pearson 1981). The Precambrian bedrock however, is only exposed in the southeastern and western edges of the wilderness (Corbett 1966). The alpine regions in the wilderness are underlain by volcanic rhyolite. Some 28 million years ago, Specimen Mountain to the southeast and Mount Lulu to the southwest erupted violently sending ash flows and pyroclastic ash falls over the area where the present day wilderness occurs (Corbett 1966, 1968). Today the volcanic material lies directly on top of the Precambrian basement rock and in places is up to 305 m thick (Pearson 1981).

Alpine glaciation during the Pleistocene carved the typical steep-walled, U-shaped valleys and formed the associated glacial deposits found in the Neota Creek and Corral Creek valleys. Altiplanation has produced many relatively rounded ridgetops and upper slopes with numerous soil polygons, rock stripes and rock streams, and hummocky, psuedo-mudflow surfaces which are the result of frost action and solifluction (Corbett 1966; Zwinger & Willard 1972).

Climate. The climate along the Front Range Continental Divide of Colorado is controlled by its mid-latitude continental location and its elevational and topographic situation (Greenland 1989). Based on data from the Joe Wright Reservoir snotel weather station, located on the northern-western boundary of the wilderness near Cameron Pass, the greatest amount of precipitation is received in the months of January, March, and April, with precipitation amounts averaging 125 mm, 122 mm, and 135 mm, respectively (Gillespie 1993). Records indicate that the driest months

are June and August, which average approximately 60 mm of precipitation each (Gillespie 1993). Average temperatures vary from approximately -10° C in December and January to 8-9° C in July and August (Gillespie 1993).

Vegetation. The Neota Wilderness is characterized by subalpine and alpine vegetation. The physiognomic communities in the subalpine of the Neota Wilderness include the spruce-fir forest, wet meadow/marsh, dry meadow, willow thicket, bogs, riparian area, lakes, and rock outcrop/talus/ boulder field sites.

The subalpine forests in the Neota Wilderness are composed primarily of *Picea engelmannii* (Parry) Engelmann and *Abies lasiocarpa* (Hooker) Nuttall. Throughout the subalpine however, occasional stands of *Pinus contorta* Douglas subsp. *latifolia* (Engelmann) Critchfield, *Populus tremuloides* Michaux, and *Pinus flexilis* James can also be found. Large areas of *Pinus contorta* are found along the northern edge of the wilderness between Joe Wright Reservoir and Bald Mountain. In these areas, as well as in some others, evidence of fire was found in the form of fallen charred trees and charcoal.

Beneath the canopy of these forests different types of ground cover exist depending on light and moisture conditions. In the drier portions of the forest, *Vaccinium scoparium* Leiberg forms the predominant ground cover with other common species including *Juniperus communis* L. subsp. *alpina* (Smith) Celakovsky, *Arnica cordifolia* Hooker, and *Packera* spp. Where moister/lower light conditions predominate, *V. scoparium* is less common and species of *Mitella*, *Ranunculus*, *Erigeron*, *Moneses*, and *Listera* are common. As more light is available grasses also become more common.

Subalpine meadows are common in the Corral Creek and Neota Creek valleys. The wet meadow/marsh communities remain wet with water flowing across them throughout most of the summer. Occasionally in late August or September portions of these areas may dry up, but generally they remain wet. Small hummocks occur, commonly topped with moss. Common species found include *Psychrophila leptosepala* (de Candolle) Weber, *Pedicularis groenlandica* Retzius, *Swertia perennis* L., *Carex aquatilis* Wahlenberg, *Gentianella acuta* (Michaux) Hiiitonen, *Carex raynoldsii* Dewey, and *Eleocharis* spp.

The dry meadows in the subalpine tend to be slightly more elevated than the wet meadows with less moisture due to better drainage. They are open areas with little or no shade. Common species include *Calamagrostis canadensis* (Michaux) P. Beauvois, *Carex albostriata* Mack., *Carex arapahoensis* Clokey, *Carex foenea* Willd., *Gentianella acuta*, *Ameroselnum lanceolata* (Torr.) Löve & Löve, *Erigeron* spp., *Valeriana edulis* Nutt., and *Juncus drummondii* Meyer.

Often associated with the wet meadow/marsh, although located closer to the forest edge or along the creeks on the valley floor, are dense willow thickets or carrs. These areas remain wet and muddy until August when they start to dry up. Common species here are *Salix planifolia* Pursh, *Salix brachycarpa* Nutt., *Betula glandulosa* Michaux, *Aconitum columbianum* Nutt., *Delphinium barbeyi* (Huth) Huth, *Castilleja sulphurea* Rydberg, and *Gentianopsis thermalis* (Kuntze) Iltis.

Subalpine bogs are open or shaded areas where seeps or underground water flows keep them constantly wet. They differ from the wet meadow/marshes by having large hummocks of *Sphagnum* moss. Common bog species include *Trollius albiflorus* (A. Gray) Rydberg, *Gentianopsis thermalis*, *Spiranthes romanzoffiana* Cham. & Schl., and *Salix planifolia*.

Rock outcrop/talus/boulder field communities often have little soil development except in small pockets in crevices and between rocks. Vegetation is often sparse and a variety of lichens cover the rocks. Common vascular plant species found in these locales include *Aquilegia coerulea* James, *Cystopteris fragilis* (L.) Bernhardi, *Luzula spicata* (L.) de Candolle, *Vaccinium scoparium*, and *Castilleja rhexifolia* Rydberg.

Riparian areas in the subalpine include both forested and unforested areas. The unforested riparian communities have been previously described as the wet meadow/marshes, willow thickets, and bogs. Common species along the forested streams include *Mertensia ciliata* (James) G. Don, *Micranthes odontoloma* (Piper) Weber, *Primula parryi* A. Gray, *Senecio triangularis* Hooker, *Cardamine cordifolia* A. Gray, and *Epilobium anagallidifolium* Lamarck.

Subalpine lakes are surrounded by woods and are generally fairly shallow with muddy or gravel bottoms. Within the lakes *Isoetes bolanderi* Engelmann, *Subularia aquatica* L., *Callitricha verna* L., and *Sparganium angustifolium* Michaux occur.

Alpine communities in the Neota Wilderness include wet, moist, and dry meadows, fellfields, krummholz, snowbank, willow thicket, boulder field, talus/cliff, and rivulet communities. Wet meadows occur in areas where seeps or continual water flows from melting snowfields above them. Common wet meadow species include *Psychrophila leptosepala*, *Pedicularis groenlandica*, *Clementsia rhodantha* (A. Gray) Rose, *Carex aquatilis* subsp. *stans* (Drejer) Hulten, and *Carex scopulorum* Holm.

Moist meadows have snow cover until mid summer. Commonly *Sibbaldia procumbens* L., *Erigeron melanocephalus* Nelson, *Salix arctica* Pallas subsp. *petraea* Anderson, *Salix reticulata* L. subsp. *nivalis* (Hooker) Löve et al., *Juncus drummondii*, *Gentianoides algida* (Pallas) Löve & Löve, *Anemonastrum narcissiflorum* (L.) Holub subsp. *zephyrum* (Nelson) Weber, *Micranthes rhomboidea* (Greene) Small, and *Veronica nutans* Bongard occur.

Dry meadows are located near the tops of leeward slopes where snow melts off quickly at the beginning of the summer. Except for occasional summer rains, these meadows receive little additional moisture the rest of the summer. Common species are *Acomastylis rossii* (R. Brown) Greene subsp. *turbinata* (Rydberg) Weber, *Rydbergia grandiflora* (Torrey & Gray) Greene, *Polemonium viscosum* Nutt., *Trifolium dasycyphllum* Torrey & Gray, *Campanula rotundifolia* L., *Gentianella acuta*, *Poa arctica* R. Brown, *Carex chalciolepis* Holm, *Carex elynoides* Holm, *Carex rupestris* Allioni subsp. *drummondii* (Dewey) Holub, and *Trisetum spicatum* (L.) Richter subsp. *congdonii* (Scribner & Merrill) Hulten.

Fellfield communities are commonly found above treeline. These are windswept, rocky expanses on windward sides of slopes where most of the snow is blown off during the winter. As a result they tend to be dry throughout the summer. Common species of the fellfields in the Neota Wilderness include *Erigeron compositus* Pursh,

Mertensia lanceolata (Pursh) de Candolle, *Erysimum capitatum* (Douglas) Greene, *Potentilla uniflora* Ledebour, *Eritrichum aretioides* (Chamisso) de Candolle, *Dryas octopetala* L. subsp. *hookeriana* (Juzepczuk) Hulten, *Paronychia pulvinata* A. Gray, *Silene acaulis* L. subsp. *subcaulescens* (Williams) Hitchcock & Maguire, *Carex rupestris* subsp. *drummondii*, *Castilleja puberula* Rydberg, *Poa arctica*, *Poa glauca* Vahl, *Oreoxis alpina* (A. Gray) Coulter & Rose subsp. *puberulenta* Weber, *Festuca brachyphylla* Schultes subsp. *coloradoensis* Fredricksen, *Trifolium nanum* Torrey, and *C. albonigra*. Fellfields associated with slopes having solifluction terracing are dominated by large mats of *D. octopetala* subsp. *hookeriana*, along with *Acomastylis rossii* subsp. *turbinata*, *Salix arctica* subsp. *petraea*, *S. reticulata* subsp. *nivalis*, and *Castilleja* spp.

Krummholz is transitional between the treeline and the alpine tundra. Trees are twisted, contorted, and flagged by the wind and often only a meter or two in height. Common species in the krummholz include *Pinus engelmannii*, *Abies lasiocarpa*, *Polemonium pulcherrimum* Hooker subsp. *delicatum* (Rydberg) Brand, *Castilleja rhexifolia*, *Juncus drummondii*, *Vaccinium scoparium*, and *Arnica cordifolia*.

In snow bank communities the growing season is very short. Often covered with snow until late in the summer, little grows in these areas. Common plants are *Ranunculus adoneus* A. Gray, *Sibbaldia procumbens*, *Vaccinium scoparium*, and a few mosses.

Alpine willow thickets are few in number and not extensive. They are located in depression areas, near the wet meadows, and below large snowfields. *Salix planifolia*, *S. brachycarpa*, *Noccaea montanum* (L.) Meyer, and *Gentianella acuta*, and in a few locations *Distegia involucrata* (Banks) Cockerell, *Aconitum columbianum*, and *Delphinium barbeyi* are common.

Boulder fields are frequent throughout the alpine. *Ciliaria austromontana* (Weigand) Weber, *Ribes cereum* Douglas, *Rubus idaeus* L. subsp. *melanolasius* (Dicke) Focke var. *aculeatissimus* Regel & Tiling, *Erigeron leiomerus* A. Gray, *Aquilegia coerulea*, *Heuchera parviflora* Nutt. and a variety of different lichen species are scattered among the boulders.

The talus slopes and cliff areas occur regularly above treeline. *Ligularia soldanella* (A. Gray) Weber, *Ligularia holmii* (Greene) Weber, *Aquilegia coerulea*, *Saxifraga rivularis* L., *Heuchera parviflora*, *Festuca brachyphylla* subsp. *coloradoensis*, *Luzula spicata*, *Carex crandellii* Gaudiger, *Castilleja rhexifolia*, and a number of different lichens are common on these unstable slopes.

Along the infrequent alpine rivulets *Psychrophila leptosepala*, *Carex aquatilis* subsp. *stans*, *Epilobium anagallidifolium*, and *Clementsia rhodantha* dominate.

FLORISTICS AND PHYTOGEOGRAPHY

Flora. The vascular flora of the Neota Wilderness was inventoried during the summers of 1992 and 1993. Identifications were verified at the University of

Northern Colorado Herbarium (GREE) and the University of Colorado Herbarium (COLO). The flora is characterized in two ways to better facilitate comparisons with other studies. The first method examines the flora of the wilderness in its entirety, incorporating species found in both the subalpine and alpine life zones. It is designated as the subalpine/alpine flora. The second method focuses on only the alpine flora.

Subalpine/Alpine Flora. A subalpine/alpine vascular flora representing 54 families, 169 genera, and 301 species of plants is found in the Neota Wilderness. The plant families contributing the greatest number of species to the flora are: Asteraceae (40 species), Poaceae (31 species), Cyperaceae (27 species), Brassicaceae (18 species), Rosaceae (16 species), Scrophulariaceae (16 species), and Saxifragaceae (14 species). Seven species endemic to Colorado/Southern Rocky Mountains occur, based on Weber & Wittman (1992). They are *Paronychia pulvinata*, *Oreoxis alpina* subsp. *puberulenta*, *Ligularia holmii*, *L. soldanella*, *Ligularia taraxacoides* (A. Gray) Weber, *Aquilegia saximontana* Rydberg, and *Primula angustifolia* Torrey.

Subularia aquatica was found growing on the muddy bottom of a subalpine lake and was reported as a new record for the state flora of Colorado (Nelson & Harmon 1993). Its discovery in Colorado extends its range southward, from known locations in Wyoming, by approximately 435–450 km, and its range eastward from a location in Utah by approximately 354 km (Nelson & Harmon 1993; Mulligan & Calder 1964).

A range extension is also reported for *Azaleastrum albiflorum* (Hooker) Rydberg. The discovery of this shrub in the Neota Wilderness represents the first discovery of *A. albiflorum* in Larimer Co., Colorado, and an extension of its range by 40–64 km east-southeast from its previously known localities in the Park Range.

No threatened or endangered species were found in the Neota Wilderness. However, ten Species of Special Concern listed by the Colorado Natural Heritage Program were found (CNHP 1996). These include *Aquilegia saximontana*, *Castilleja puberula*, *Chionophila jamesii* Benth., *Draba crassa* Rydberg, *Draba fladnizensis* Wulfen, *Draba lonchocarpa* Rydberg, *Draba streptobrachia* Price, *Azaleastrum albiflorum*, *Muscaria monticola* Small, and *Subularia aquatica*.

Alpine Flora. The alpine vascular flora represents 39 families, 118 genera, and 203 species in the Neota Wilderness. The plant families contributing the greatest number of species to the alpine flora are: Asteraceae (37 species), Cyperaceae (15 species), Poaceae (14 species), Brassicaceae (13 species), Scrophulariaceae (12 species), Rosaceae (12 species), and Saxifragaceae (12 species). The same seven species mentioned above in the Subalpine/Alpine Flora section as endemic to Colorado/Southern Rocky Mountains occur in the alpine flora of the Neota Wilderness. No threatened or endangered species have been found in the alpine flora; however, the same State Species of Special Concern mentioned above in the Subalpine/Alpine Flora section apply here, with the exception of *Azaleastrum albiflorum* and *Subularia aquatica* which were found only in the subalpine.

Floristic Comparisons. Floristic comparisons between the subalpine/alpine and alpine Neota Wilderness floras and other floras in Colorado use the Sorenson coefficient of similarity (Mueller-Dombois & Ellenberg 1974; Hogan 1992). The

Sorensen coefficient is an index equal to $[(2C/A+B) \times 100]$ where C equals the number of species shared by both sites, and A and B are the total number of species from each respective site.

Floristic comparisons were made using the Sorensen index value between the subalpine/alpine Neota Wilderness flora and the subalpine/alpine floras of the Eagles Nest Wilderness (60.5%; Hogan 1992), Needles Mountains (59.3%, Michner 1964) and Robinson Basin (53.6%, Bathke 1968). Floristic comparisons were also made between the alpine Neota flora and the alpine floras of the Indian Peaks Wilderness area (68.28%, Komarkova 1979), Sawatch Range (68.02%; Hartman & Rottman 1988), Ruby Range (67.30%; Hartman & Rottman 1987), Mt. Bross (58.86%; Hartman & Rottman 1985a), San Juan Mountains (64.66%; Hartman & Rottman 1985b), and Specimen Mountain (64.92%; McNeal 1976). These comparisons show the subalpine/alpine flora and alpine flora of the Neota Wilderness to have a relatively high similarity (54-68%) with the floras of other mountain ranges in Colorado. This agrees with the findings of Hartman & Rottman (1988), who indicated that most of the differences that exist between alpine floras in Colorado can be attributed to distributional ranges of taxa or substrate and microhabitat differences.

Phytogeography. The flora of the Neota Wilderness can be characterized phytogeographically using flora element and geographic subelement categories. This follows the method described and used by Komarkova (1979) and used by other researchers in Colorado in recent years (Hartman & Rottman 1985a, 1985b, 1987, 1988; Hogan 1992). Floristic elements represent both the latitudinal (arctic, boreal) and altitudinal (alpine, montane) distribution of the taxa. The geographic subelement denotes the geographic range of the taxa, beginning with the broadest distribution (circumpolar) and ending with the most restricted (Colorado).

The phytogeographic distribution of the subalpine/alpine flora (Table 1) reveals that the largest floristic element in the Neota Wilderness flora is the Boreal-Montane element (32.6%). The Arctic-Alpine element (20.3%) is the lowest percentage. Phytogeographic subelement distribution of the subalpine/alpine flora (Table 1) shows that the largest geographic subelement in the Neota Wilderness flora is the Western North America subelement (32.6%) followed by the Circumpolar subelement (22.3%). The lowest percentage of the flora is made up of the North American-European subelement (1.0%).

The phytogeographic distribution of the alpine flora of the Neota Wilderness reveals that the largest flora element is the Alpine element (34.5%) (Table 2). The lowest percentage of the alpine flora is composed of the Montane element (15.8%). The phytogeographic subelement distribution of the alpine flora (Table 2) shows that the Western North American subelement comprises the largest percentage of the alpine flora (33.0%) followed by the Circumpolar subelement (19.7%). The lowest percentage of the alpine flora is from the North American-European subelement (0.5%).

A comparison of the subalpine/alpine and alpine flora elements in the Neota flora reveals that in both cases approximately 50% of the flora have a strong tie to the boreal and arctic floras found at higher latitudes. It is also apparent that as the base elevation of a site decreases (adding the subalpine flora to the alpine flora), the percentage of

Alpine and Arctic-Alpine species decreases and an increase in the percentage of Montane and Boreal-Montane element species occurs. A similar comparison of the subelement data shows that the Neota flora is composed of primarily Western North American and Circumpolar subelement species. The high percentage of North American-Asiatic species as compared to North American-European species underscores the floristic relationship that exists between the Rocky Mountains and Asiatic mountains. This has been discussed by others (Weber 1965, 1987; Komarkova 1979). These generalizations are accurate for the subalpine/alpine and alpine floras across the state when different floristic studies have been compared across Colorado (Nelson 1993).

Table 1. Phytogeographic distribution of subalpine/alpine flora of the Neota Wilderness.

Phytogeographic Category	# Species	Percent
Element		
Arctic-Alpine (AA)	61	20.3
Alpine (A)	80	26.6
Boreal-Montane (BM)	98	32.6
Montane (M)	62	20.5
Subelement		
Circumpolar (C)	67	22.3
North American (NA)	37	12.3
Western North American (WNA)	98	32.6
Rocky Mountain (RM)	38	12.6
Southern Rocky Mountains (SRM)	26	8.6
Colorado (CO)	5	1.7
North American-Asiatic (NAA)	27	9.0
North American-European (NAE)	3	1.0

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Table 2. Phytogeographic distribution of the alpine flora of the Neota Wilderness.

Phytogeographic Category	# Species	Percent
Element		
Arctic-Alpine (AA)	51	25.1
Alpine (A)	70	34.5
Boreal-Montane (BM)	50	24.6
Montane (M)	32	15.8
Subelement		
Circumpolar (C)	40	19.7
North American (NA)	21	10.3
Western North American (WNA)	67	33.0
Rocky Mountains (RM)	27	13.3
Southern Rocky Mountains (SRM)	23	11.3
Colorado (CO)	5	2.5
North American-Asiatic (NAA)	19	9.4
North American-European (NAE)	1	0.5

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NEOTA WILDERNESS SPECIES LIST

Nomenclature follows that given in Weber & Wittman (1992). A complete voucher collection of the flora is located in the herbarium at the University of Northern

Colorado (GREE). In addition, duplicates of some specimens are also found in the University of Colorado - Boulder herbarium (COLO). As with all floras, this is a working flora and although pains were taken to explore all the habitats found in the area a number of times throughout the two summers, it is still possible that some plants may have been missed. This study provides a baseline of floristic data for the wilderness to which additions may be made. Phytogeographic codes follow those presented in Tables 1 and 2. The letter (E) preceding some species indicates an endemic species.

CATALOGUE OF VASCULAR PLANT TAXA OF THE NEOTA WILDERNESS, COLORADO

MICROPHYLLOPHYTA

Isoetaceae

Isoetes bolanderi Engelmann - BM, WNA

Lycopodiaceae

Lycopodium annotinum L. - BM, C

Selaginellaceae

Selaginella densa Rydberg - A, WNA

SPHENOPHYTA (ARTHROPHYTA)

Equisetaceae

Equisetum arvense L. - BM, C

PTERIDOPHYTA

Athyriaceae

Cystopteris fragilis (L.) Bernhardi - AA, C

Cryptogrammaceae

Cryptogramma acrostichoides R. Brown - BM, NAA

Woodsiaceae

Woodsia scopulina D.C. Eaton - BM, NA

CONIFEROPHYTA

Cupressaceae

Juniperus communis L. subsp. *alpina* (Smith) Celakovsky - BM, C

Pinaceae

Abies lasiocarpa (Hooker) Nuttall - BM, WNA; *Picea engelmannii* (Parry) Engelmann - BM, WNA; *Pinus contorta* Douglas subsp. *latifolia* (Engelmann) Critchfield - BM, WNA; *Pinus flexilis* James - BM, WNA

ANTHOPHYTA-DICOTYLEDONEAE (DICOTS)

Adoxaceae

Adoxa moschatellina L. - BM, C

Alsinaceae

Cerastium beeringianum Chamisso & Schlechtendal subsp. *earlei* (Rydberg) Hulten - A, RM; *Cerastium stricta* L. emend Haenke - BM, C; *Eremogone fendleri* (A. Gray) Ikonnikov - A, SRM; *Lidia obtusiloba* (Rydberg) Löve & Löve - AA,

NAA; (E) *Paronychia pulvinata* A. Gray - A, SRM; *Sagina saginoides* (L.) Karstens - AA, C; *Stellaria longipes* Goldie - BM, NA; *Stellaria umbellata* Turczaninow - A, NAA; *Tryphane rubella* (Wahlenburg) Reichenbach - AA, C

Apiaceae

Angelica grayi (Coulter & Rose) Coulter & Rose - A, SRM; *Ligusticum porteri* Coulter & Rose - M, WNA; (E) *Oreoxis alpina* (A. Gray) Coulter & Rose subsp. *puberulenta* Weber - A, CO; *Oreoxis alpina* (A. Gray) Coulter & Rose - A, SRM; *Osmorhiza depauperata* Phillipi - M, NA; *Oxypolis fendleri* (A. Gray) Heller - M, SRM; *Pseudocymopteris montanus* (A. Gray) Coulter & Rose - M, SRM

Asteraceae

Achillea lanulosa Nuttall - M, WNA; *Agoseris aurantiaca* (Hooker) Greene - BM, WNA; *Agoseris glauca* (Pursh) Rafinesque - BM, NA; *Anaphalis margaritacea* (L.) Bentham & Hooker - BM NAA; *Antennaria corymbosa* Nelson - M, WNA; *Antennaria media* Greene - AA, WNA; *Antennaria rosea* Greene - BM, WNA; *Antennaria umbrinella* Rydberg - A, WNA; *Arnica cordifolia* Hooker - BM, WNA; *Arnica mollis* Hooker - BM, NA; *Arnica rydbergii* Greene - BM, WNA; *Artemisia arctica* Lessing subsp. *saxicola* (Rydberg) Hulten - AA, NAA; *Artemisia michauxiana* Besser - BM, WNA; *Artemisia scopulorum* A. Gray - A, RM; *Aster foliaceus* Lindley - M, WNA; *Chlorocrepis tristis* (Willdenow) Löve & Löve subsp. *gracilis* (Hooker) Weber - M, WNA; *Cirsium centaureae* (Rydberg) Schwann - M, RM; *Cirsium tweedyi* (Rydberg) Petrak - A, RM; *Erigeron compositus* Pursh - BM NA; *Erigeron elatior* (A. Gray) Greene - M, SRM; *Erigeron leiomerus* A. Gray - M, RM; *Erigeron melanocephalus* Nelson - A, SRM; *Erigeron peregrinus* (Banks) Greene subsp. *callianthemus* (Greene) Cronquist - A, SRM; *Erigeron pinnatisectus* (A. Gray) Nelson - A, SRM; *Erigeron simplex* Greene - A, WNA; *Heterotheca pumila* (Greene) Semple - M, RM; (E) *Ligularia holmii* (Greene) Weber - A, RM; (E) *Ligularia soldanellea* (A. Gray) Weber - A, CO; (E) *Ligularia taraxacoides* (A. Gray) Weber - A, SRM; *Packera dimorphophylla* (Greene) Weber & Löve - A, RM; *Packera wernyiifolia* (A. Gray) Weber & Löve - A, RM; *Rydbergia grandiflora* (Torrey & Gray) Greene - A, RM; *Senecio atratus* Greene - M, SRM; *Senecio crassulus* A. Gray - M, WNA; *Senecio fremontii* Torrey & Gray var. *blitoides* (Greene) Cronquist - A, WNA; *Senecio triangularis* Hooker - BM, WNA; *Solidago multiradiata* Aiton subsp. *scopulorum* (A. Gray) Weber - BM, WNA; *Taraxacum officinale* H.G. Weber - BM, C; *Taraxacum ovinum* Rydberg - AA, C; *Tonestus pygmaeus* (Torrey & Gray) Nelson - A, RM

Betulaceae

Betula glandulosa Michaux - BM NA

Boraginaceae

Eritrichium aretioides (Chamisso) de Candolle - AA, NAA; *Mertensia ciliata* (James) G. Don - M, WNA; *Mertensia lanceolata* (Pursh) de Candolle - A, WNA

Brassicaceae

Boechera drummondii (A. Gray) Löve & Löve - BM, NA; *Cardamine cordifolia* A. Gray - M, WNA; *Cardamine pennsylvanica* Muhlenberg - BM, NA; *Draba albertina* Greene - AA, NAE; *Draba aurea* Vahl. - AA, WNA; *Draba cana* Rydberg - AA, C; *Draba crassa* Rydberg - A, RM; *Draba crassifolia* Graham - AA, NAE; *Draba fladnizensis* Wulfen - AA, C; *Draba lonchocarpa* Rydberg - A, NAA; *Draba nemorosa* L. - BM, C; *Draba streptobrachia* Price - A, CO; +*Draba streptocarpa* A. Gray - A, SRM; *Erysimum capitatum* (Douglas) Greene - A, WNA; *Noccaea montana* (L.) Meyer - M, WNA; *Rorippa curvipes* Greene var. *alpina* (Watson)

Stuckey - A, RM; *Smelowskia calycina* (Stephans) Meyer - AA, NAA; *Subularia aquatica* L. - BM, C

Callitrichaceae
Callitricha verna L. - BM, C

Campanulaceae
Campanula rotundifolia L. - BM, C; *Campanula uniflora* L. - AA, C

Caprifoliaceae
Distegia involucrata (Banks) Cockerell - BM, NA; *Sambucus microbotrys* Rydberg - BM, NA

Caryophyllaceae
Gastrolychnis drummondii (Hooker) Löve & Löve - BM, Nal; *Gastrolychnis kingii* (Watson) Weber - A, SRM; *Silene acaulis* L. subsp. *subcaulescens* (Williams) Hitchcock & Maguire - AA, NAA

Crassulaceae
Amerosedum lanceolatum (Torrey) Löve & Löve - A, WNA; *Clementsia rhodantha* (A. Gray) Rose - A, RM; *Rhodiola integrifolia* Rafinesque - AA, NAA

Ericaceae
Arctostaphylos uva-ursi (L.) Sprengel - BM, C; *Azaleastrum albiflorum* (Hooker) Rydberg - M, WNA; *Gaultheria humifusa* (Graham) Rydberg - BM, WNA; *Kalmia microphylla* (Hooker) Heller - BM, WNA; *Vaccinium caespitosum* Michaux - BM, NA; *Vaccinium scoparium* Leiberg - BM, WNA

Fabaceae
Trifolium dasypodium Torrey & Gray - A, RM; *Trifolium nanum* Torrey - A, RM; *Trifolium parryi* A. Gray - A, RM; *Vicia americana* Muhlenberg - BM, NA

Gentianaceae
Chondrophyllea prostrata (Haenke) J.P. Anderson - AA, C; *Comastoma tenellum* (Rottboell) Toyokuni - AA, C; *Gentianella acuta* (Michaux) Hiiton - BM, NAA; *Gentianoides algida* (Pallas) Löve & Löve - AA, NAA; *Gentianopsis barbellata* (Engelmann) Iltis - A, SRM; *Gentianopsis thermalis* (Kuntze) Iltis - A, RM; *Pneumonanthe parryi* (Engelmann) Greene - M, RM; *Swertia perennis* L. - A, C

Geraniaceae
Geranium richardsonii Fisher & Trautvetter - M, WNA

Grossulariaceae
Ribes cereum Douglas - M, WNA; *Ribes coloradoense* Coville - M, SRM; *Ribes montigenum* McClatchie - M, WNA

Helleboraceae
Aconitum columbianum Nuttall - BM, WNA; *Aquilegia coerulea* James - M, RM; *Aquilegia saximontana* Rydberg - A, CO; *Delphinium barbeyi* (Huth) Huth. - M, SRM; *Psychrophila leptosepala* (de Candolle) Weber - A, WNA; *Trollius albiflorus* (A. Gray) Rydberg - M, WNA

Hydrophyllaceae
Phacelia sericea (Graham) A. Gray - A, WNA

Monotropaceae
Hypopitys monotropa Crantz - BM, C

Onagraceae
Chamerion daniellii (Daniels) D. Löve - BM, C; *Epilobium anagallidifolium* Lamarck - AA, C; *Epilobium halleanum* Haussknecht - BM, WNA; *Epilobium hornemannii* Reichenbach - BM, C; *Epilobium lactiflorum* Haussknecht - BM, C; *Gayophytum diffusum* Torrey & Gray subsp. *parviflorum* Lewis & Szwedkowski - M, WNA

Parnassiaceae

Parnassia fimbriata Banks - BM, WNA

Plantaginaceae

Plantago tweedyi A. Gray - M, RM

Polemoniaceae

Polemonium pulcherrimum Hooker subsp. *delicatum* (Rydberg) Brand - M, NAA;

Polemonium viscosum Nuttall - A, WNA

Polygonaceae

Bistorta bistortoides (Pursh) Small - A, WNA; *Bistorta vivipara* (L.) S. Gray -

AA, C; *Eriogonum subalpinum* Greene - M, WNA; *Eriogonum jamesii* Bentham

var. *xanthus* (Small) Reveal - M, WNA; *Oxyria digyna* (L.) Hill - AA, C;

Polygonum douglasii Greene - M, WNA; *Rumex densiflorus* Osterhout - M, RM

Portulacaceae

Oreobroma pygmaea (A. Gray) Howell - A, WNA; *Claytonia megarhiza* (A. Gray)

Pursh - A, RM

Primulaceae

Androsace septentrionalis L. - A, C; *Dodecatheon pulchellum* (Rafinesque) Merrill

- BM, WNA; *Primula angustifolia* Torrey - A, SRM; *Primula parryi* A. Gray - A,

RM

Pyrolaceae

Moneses uniflora (L.) S. Gray - BM, C; *Orthilia secunda* (L.) House - BM, NAA;

Pyrola minor L. - BM, C

Ranunculaceae

Anemonastrum narcissiflorum (L.) Holub subsp. *zephyrum* (Nelson) Weber - A, SRM; *Anemone multifida* Poiret subsp. *globosa* (Nuttall) Torrey & Gray - BM, NA; *Pulsatilla patens* (L.) Miller subsp. *hirsutissima* Zamel - BM, NA; *Ranunculus adoneus* A. Gray - A, RM; *Ranunculus alismifolius* Geyer var. *montanus* Watson - BM, WNA; *Ranunculus eschscholtzii* Schlechtendal - AA, NAA; *Ranunculus gmelinii* de Candolle var. *hookeri* (D. Don) Benson - BM, NAA; *Ranunculus reptans* L. - BM, C

Rosaceae

Acomastylis rossii (R. Brown) Greene subsp. *turbinata* (Rydberg) Weber - AA, NAA; *Amelanchier alnifolia* Nuttall - BM, WNA; *Dryas octopetala* L. subsp. *hookeriana* (Juzepczuk) Hulten - AA, C; *Drymocallis glandulosa* (Lindley) Rydberg - M, WNA; *Erythrocoma triflora* (Pursh) Greene - M, NA; *Fragaria virginiana* Miller subsp. *glaucia* (Watson) Staudt - M, C; *Pentaphylloides floribunda* (Pursh) A. Löve - BM, C; *Potentilla diversifolia* Lehmann - A, WNA; *Potentilla hippiana* Lehmann - M, WNA; *Potentilla ovina* Macoun - M, WNA; *Potentilla pensylvanica* L. - BM, NA; *Potentilla rubricaulis* Lehmann - AA, NA; *Potentilla uniflora* Ledebour - AA, NAA; *Rosa woodsia* Lindley - BM, NA; *Rubus idaeus* L. subsp. *melanolasius* (Dicke) Focke var. *aculeatissimus* Regel & Tiling - BM, C; *Sibbaldia procumbens* L. - AA, C

Rubiaceae

Galium trifidum (L.) subsp. *brevipes* (Fernald & Wiegand) Löve & Löve - BM, C

Salicaceae

Populus balsamifera L. - BM, NA; *Populus tremuloides* Michaux - BM, NA; *Salix arctica* Pallas subsp. *petraea* Anderson - AA, C; *Salix boothii* Dorn - M, RM; *Salix brachycarpa* Nuttall - BM, NA; *Salix planifolia* Pursh - BM, NA; *Salix reticulata* L. subsp. *nivalis* (Hooker) Löve et al. - A, WNA

Saxifragaceae

Ciliaria austromontana (Weigand) Weber - M, WMA; *Heuchera bracteata* (Torrey) Seringe - A, SRM; *Heuchera parvifolia* Nuttall - M, RM; *Hirculus platysepalus* (Trautvetter) Weber subsp. *crandallii* (Gandoger) Weber - A, SRM; *Hirculus serpylifolius* (Pursh) Weber subsp. *crysanthus* (A. Gray) Weber - AA, NAA; *Micranthes odontoloma* (Piper) Weber - BM, WNA; *Micranthes rhomboidea* (Greene) Small - M, WNA; *Mitella pentandra* Hooker - BM, WNA; *Mitella stauropetala* Piper var. *stenopetala* (Piper) Rosendahl - M, RM; *Muscaria delicatula* Small - AA, C; *Muscaria monticola* Small - AA, C; *Saxifraga cernua* L. - AA, C; *Saxifraga hyperborea* R. Brown subsp. *debilis* (Engelmann) Löve et al. - A, WNA; *Saxifraga rivularis* L. - AA, C

Scrophulariaceae

Besseya alpina (A. Gray) Rydberg - A, SRM; *Castilleja miniata* Douglas - BM, WNA; *Castilleja occidentalis* Torrey - A, RM; *Castilleja puberula* Rydberg - A, CO; *Castilleja rhexifolia* Rydberg - M, RM; *Castilleja sulphurea* Rydberg - M, RM; *Chionophila jamesii* Benthams - A, SRM; *Mimulus guttatus* de Candolle - BM, WNA; *Pedicularis bracteosa* Benthams subsp. *paysoniana* (Pennell) Weber - M, RM; *Pedicularis groenlandica* Retzius - AA, RM; *Pedicularis parryi* A. Gray - A, RM; *Pedicularis racemosa* Douglas subsp. *alba* Pennell - M, WNA; *Penstemon confertus* Douglas subsp. *procerus* (Douglas) Clark - BM, WNA; *Penstemon whippleanus* A. Gray - M, RM; *Veronica americana* (Rafinesque) Schweinitz - BM, NAA; *Veronica nutans* Bongard - AA, WNA

Valerianaceae

Valeriana edulis Nuttall - M, WNA

Violaceae

Viola labradorica Schrank - BM, NA; *Viola renifolia* A. Gray var. *brainerdii* (Greene) Fernald - BM, NA

Viscaceae

Arceuthobium americanum Nuttall - BM, WNA

ANTHOPHYTA-MONOCOTYLEDONEAE (MONOCOTS)

Cyperaceae

Carex albonigra Mack. - AA, WNA; *Carex aquatilis* Wahlenberg - AA, C; *Carex aquatilis* Wahlenberg subsp. *stans* (Drejer) Hulten - AA, C; *Carex arapahoensis* Clokey - A, SRM; *Carex brevipes* Boott - BM, WNA; *Carex buxbaumii* Wahlenberg - BM, NAE; *Carex capillaris* L. - AA, C; *Carex chalciolepis* Holm - A, WNA; *Carex crandallii* Gandoger - A, WNA; *Carex eggelstonii* Mack. - M, SRM; *Carex elynoides* Holm - A, WNA; *Carex foenea* Willdenow - BM, NA; *Carex hoodii* Boott - M, WNA; *Carex illota* Bailey - A, WNA; *Carex jonesii* Bailey - M, WNA; *Carex lachenalii* Schkuhr - AA, C; *Carex nigricans* Meyer - AA, NAA; *Carex parryana* Dewey subsp. *hallii* Murray - BM, NA; *Carex periglobosa* Mack - A, SRM; *Carex praeceptorum* Mack. - A, WNA; *Carex raynoldssii* Dewey - M, WNA; *Carex rupestris* Allioni subsp. *drummondii* (Dewey) Holub - A, WNA; *Carex scopolorum* Holm - A, WNA; *Eleocharis bolanderi* A. Gray - M, WNA; *Eleocharis palustris* (L.) Roemer & Schultes - BM, C; *Eleocharis quinqueflora* (Hartman) Schwartz - BM, C; *Eriophorum angustifolium* Honekeny - AA, C.

Juncaceae

Juncus biglumis L. - AA, C; *Juncus drummondii* Meyer - A, WNA; *Juncus mertensianus* Bongard - A, NAA; *Juncus nevadensis* Watson - M, WNA; *Juncus triglumis* L. - AA, C; *Luzula comosa* E. Meyer - M, NA; *Luzula parviflora* (Erhart) Desvaux - BM, C; *Luzula spicata* (L.) de Candolle - A, RM

Liliaceae

Erythronium grandiflorum Pursh - M, RM; *Lloydia serotina* Reichenbach - AA, C

Melanthiaceae

Anticlea elegans (Pursh) Rydberg - AA, WNA

Orchidaceae

Corallorrhiza maculata Rafinesque - BM, NA; *Corallorrhiza trifida* Chatelain - BM, C; *Goodyera oblongifolia* Rafinesque - BM, NA; *Limnochis dilatata* Rydberg subsp. *albiflora* (Chamisso) Löve & Simon - BM, NA; *Listera cordata* (L.) R. Brown subsp. *nephrophylla* (Rydberg) Löve & Löve - BM, C; *Spiranthes romanzoffiana* Cham. & Schl. - BM, NA

Poaceae

Agrostis humilis Vasey - A, WNA; *Agrostis mertensii* Trinius - AA, C; *Agrostis scabra* Willdenow - BM, NA; *Agrostis variabilis* Rydberg - A, WNA; *Alopecurus aequalis* Sobol - AA, C; *Alopecurus alpinus* Smith - AA, C; *Bromopsis canadensis* (Michaux) Holub - BM, NAA; *Calamagrostis canadensis* (Michaux) P. Beauvois - BM, NAA; *Calamagrostis purpurascens* R. Brown - AA, NAA; *Danthonia intermedia* Vasey - BM, NAA; *Deschampsia caespitosa* (L.) P. Beauvois - BM, C; *Elymus elymoides* (Rafinesque) Swezey - M, WNA; *Elymus scribneri* (Vasey) Jones - A, WNA; *Elymus trachycaulus* (Link) Gould - AA, NA; *Festuca baffinensis* Poulin - AA, NA; *Festuca brachyphylla* Schultes subsp. *coloradoensis* Frederiksen - AA, NAA; *Hierochloe hirta* (Shrank) Borbas subsp. *arctica* (Presl) Weimarck - AA, C; *Koeleria macranthes* (Ledebour) Schultes - M, C; *Phleum commutatum* Gaudin - AA, C; *Poa alpina* L. -AA, C; *Poa arctica* R. Brown - AA, WNA; *Poa cusickii* Vasey subsp. *epilis* (Scribner) Weber - A, WNA; *Poa glauca* Vahl - A, WNA; *Poa glaucifolia* Scribner & Williams - M, RM; *Poa nemoralis* L. subsp. *interior* (Rydberg) Butter & Abbe - BM, NA; *Poa nervosa* (Hooker) Vasey - M, WNA; *Poa reflexa* Vasey & Scribner - A, WNA; *Poa secunda* Presl. - M, WNA; *Torreyochoa pauciflora* (Presl.) Church - BM, WNA; *Trisetum spicatum* (L.) Richter - AA, C; *Trisetum spicatum* (L.) Richter subsp. *congdonii* (Scribner & Merrill) Hulten - AA, C

Sparganiaceae

Sparganium angustifolium Michaux - AA, C

Uvulariaceae

Streptopus fassettii Löve & Löve - BM, WNA

TAXONOMIC AND NOMENCLATURAL COMMENTS ON THE TRITICEAE IN NORTH AMERICA

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ABSTRACT

Miscellaneous information concerning the Triticeae in North America is presented. New combinations are provided for three subspecies of *Elymus elymoides*, one subspecies of *Leymus mollis*, two species of *Thinopyrum*, and four intergeneric hybrids. *Agropyron* is described as a well-circumscribed genus, whose treatment at the species level in North America is complicated by human manipulation. *Elymus* is interpreted as including *E. repens*, the type species of *Elytrigia*. A description of *Thinopyrum* is provided and the genus expanded to include two introduced species sometimes included in *Agropyron* or *Elytrigia*. Evidence suggesting that *Elymus californicus* should be transferred to *Leymus* is reviewed. Finally, a list of several unpublished theses involving systematic research on North American Triticeae is given.

KEY WORDS: *Agropyron*, *Elymus elymoides*, *Elymus repens*, *Elymus stebbinsii*, *Thinopyrum*, \times *Elyhordeum pilosilemma*, North America, taxonomy, nomenclature, Triticeae, Poaceae

INTRODUCTION

This paper presents miscellaneous matters concerning the treatment of the Triticeae in the forthcoming *Manual for Grasses of the Continental United States and Canada* (Barkworth *et al.*, in prep.). The items included are: taxonomic treatment of *Agropyron*, *Elytrigia*, *Thinopyrum*, and *Leymus*, valid publication of names for the infraspecific taxa of *Elymus elymoides*, comments on recent findings concerning *Elymus stebbinsii* and *Elymus californicus*, and transfer of \times *Agrohordeum pilosilemma* to \times *Elyhordeum pilosilemma*. The items are treated in the above order. Illustrations of all the taxa will be included in the Manual.

Agropyron

One of the few points of agreement concerning the generic treatment of perennial Triticeae is that *Agropyron* Gaertner should be restricted to the "crested wheatgrasses". Starting in the nineteenth century, the departments of agriculture in the United States and Canada have been bringing accessions of *Agropyron* into North America, looking for grasses that would increase the grazing potential of arid regions in the west. These accessions were planted in experiment stations where they became the focus of breeding programs designed to develop cultivars appropriate to different parts of the continent. These programs included controlled and uncontrolled hybridization and attempts to increase the fertility of sterile hybrids by artificially doubling their chromosome complement and selecting for the most fertile offspring.

The result is a taxonomic dilemma. As Dewey stated (1986), "... taxa introduced into North America soon lose their taxonomic identity and genetic integrity because of extensive intercrossing that occurs in nursery situations where many accessions are grown in close proximity to each other", and "[many North American introductions] are genetically mixed by hybridization and single accessions often contain several morphological forms" (*ibid.*, p. 38). After careful consideration of specimens, including type specimens, at LE (herbarium codes from Holmgren *et al.* 1990) as well as North American plant material, Dewey concluded that the best solution was to treat North American material as belonging to one of three species, *Agropyron cristatum* (L.) Gaertner, *A. desertorum* (Fischer ex Link) Schultes, or *A. fragile* (Roth) P. Candargy. He summarized their distinguishing characters in a table (Table 1). He also stated, however, that "Classification of crested wheatgrass accessions or individual plants into one of the three species will often be difficult and unsatisfying".

I wholeheartedly agree with the last statement. Unfortunately, because crested wheatgrass has been widely planted on rangelands in arid regions of North America, taxonomists are often asked to identify it. I generally try to persuade those asking for identifications to be happy with *Agropyron* sp. If a binomial is required, Dewey's approach is practical, albeit artificial. Providing names at a lower taxonomic rank would require a better understanding than I have of the variation in *Agropyron* in Eurasia and an examination of the numerous type specimens involved. It seems best to let sleeping dogs lie. *Agropyron* in North America should be considered an example of human-induced despeciation.

Elytrigia and *Thinopyrum*

In the past, Tsvelev (1976), Löve (1984), Dewey (1984), and Barkworth (1989) included *Elymus repens* in *Elytrigia*, of which it is the type species. According to Tsvelev (1976), *Elytrigia* differed from *Elymus* in having completely sessile spikelets, a tardily or non-disarticulating rachilla, and glumes that were scabrous only on the midrib, had a transverse indentation near the base and well developed keel towards the tip. He included in the genus species that Dewey (1984) and Barkworth (1989) treated in *Pseudoroegneria* or *Thinopyrum*.

A major factor in Dewey's and my decisions was the observation that Tsvelev's treatment of the Triticeae tended to concur with relationships suggested by cytogenetic

data and Tsvelev's knowledge of a wide range of Triticeae. Others prefer to include the species, and Tsvelev's other species of *Elytrigia*, in *Elymus* (e.g., Melderis 1978; Cope 1982). Melderis, in explaining his decision, cited the morphological continuity between segregate genera such as *Pseudoroegneria*, *Elymus*, *Elytrigia*, and *Thinopyrum* and the frequency with which hybrids between these genera occur.

Despite my treatment of *Elymus repens* as a species of *Elytrigia*, I recognized that its overall appearance, if one excludes the rhizomatous character, is similar to that of other species of *Elymus*. I admit, however, that my decision to include *Elymus repens* in *Elymus* was made when it was discovered that it is genomically similar to other species of *Elymus* (Assadi & Runemark 1995). Genomic constitution, by itself, should not determine the generic placement of a species, but if other data have one sitting on the fence (a position that is not evident from one's nomenclatural practice), a single character may have more apparent importance than would otherwise be the case.

Elymus repens differs from most species occurring in North America in being a hexaploid with a genomic composition of StStH (genomic symbols are based on recommendations in Wang *et al.* 1996). *Elymus transhyrcanus* Tzvelev, a Transcaucasian and central Asian species, is the only other StStH species known (Dewey 1972), but there are many species of Triticeae for which the genomic composition is not yet known.

The inclusion of *Elymus repens* in *Elymus* raises the question of how to treat other species that have been included in *Elytrigia*. Melderis (1978) and Assadi & Runemark (1995) include them in *Elymus*, but I prefer to continue recognizing both *Thinopyrum* sensu D.R. Dewey (1986) and *Pseudoroegneria* (Carlson & Barkworth 1998). This made it necessary to review the two other species of *Elytrigia* reported from North America, *Elytrigia pungens* (Pers.) Tutin and *Elytrigia pycnantha* (Godron) A. Löve.

Thinopyrum consists of species with solitary, trullate spikelets with stiff, thick, acute to truncate glumes, tardily or non-disarticulating rachillas, and long anthers. Both *Elytrigia pungens* and *Elytrigia pycnantha* species, but not *Elymus repens* fall within this circumscription. I therefore propose the following combinations:

***Thinopyrum pungens* (Pers.) Barkworth, comb. nov.** BASIONYM: *Triticum pungens* Pers., *Syn. Pl.* 1:109 (1805).

SYNONYMS: *Agropyron pungens* (Pers.) Roemer & Schultes, *Syst. Veg.* 2:753 (1817); *Elytrigia pungens* (Pers.) Tutin, *Watsonia* 2:186 (1952); *Elymus pungens* (Pers.) Melderis, *Bot. J. Linn. Soc.* 76:380 (1978); *Psammopyrum pungens* (Pers.) A. Löve, *Veröff. Geobot. Inst. ETH Stiftung Rübel Zürich* 87:50 (1986).

***Thinopyrum pycnanthum* (Godron) Barkworth, comb. nov.** BASIONYM: *Triticum pycnanthum* Godron, *Mém. Soc. Emul. Doubs.*, sér. 2, 5:10 (1854).

SYNONYMS: *Agropyron pycnanthum* (Godron) Gren. in Gren. & Godron, *Fl. France* 3:606 (1856); *Elymus pycnanthus* (Godron) Melderis, *Bot. J. Linn. Soc.* 76:378 (1978); *Elytrigia pycnantha* (Godron) A. Löve, *Taxon* 29:351 (1980).

***Triticum littorale* Host, *Icones Descr. Gram. Austriac.* 4:5 (1809), *non* Pallas (1773); *Triticum pungens* auct., *non* Pers. (1895); *Agropyron pungens* auct., *non* Roemer & Schultes (1817).**

Table 1. Comparison of *Agropyron fragile*, *A. desertorum*, and *A. cristatum* sensu lato, based on Tsvelev (1976), Dewey (1986), and personal observation.

Character	<i>A. fragile</i>	<i>A. desertorum</i>	<i>A. cristatum</i>
Spike length	3-15 cm	2-7 cm	(1.5)2-6(8) cm
Spike width	0.5-1 cm	0.5-1 cm	0.8-2.3 cm
Spike shape	Linear	Narrowly lanceolate to oblong or broadly linear	Oblong to broadly oblong
Spikelets (below midlength)	Appressed or diverging at an angle of less than 30°	Diverging at an angle of 25-45°	Diverging at an angle of 45-90°
Glumes	Appressed to lemmas	Appressed to lemmas	Not appressed to lemmas
Lemma apex	Unawned, sometimes with a mucro up to 1 mm long	With an awn 1-4 mm long	With an awn up to 5 mm long

Neither species has been studied genomically, but Assadi & Runemark (1995, p. 201) state that "[they] obviously have a J, with the other genomes not yet satisfactorily determined". All species of *Thinopyrum* for which the information is available have at least one copy of this genome (or its variant, the J' genome), sometimes in combination with other genomes (Assadi & Runemark 1995).

Elymus elymoides

Elymus elymoides (Raf.) Swezey is sometimes included in *Sitanion* (Hitchcock 1951; Clayton & Renvoize 1986). Species of *Sitanion* differ from other species of *Elymus* primarily in their articulating rachis and the long, arcuately diverging awns of their glumes and lemmas. This combination of characters promotes wind dispersal of the diaspores over open, relatively bare ground. *Sitanion* was last revised by Wilson (1963) but, in my treatment for the Jepson Manual (Barkworth 1993), I followed Holmgren & Holmgren (1977) in recognizing two species, one with four infraspecific taxa, but chose to include the species in *Elymus* and treat the infraspecific taxa as subspecies rather than varieties. Unfortunately, I managed to overlook the need to publish the new combinations. They are presented here for the first time:

Elymus elymoides (Raf.) Swezey subsp. *brevifolius* (J.G. Sm.) Barkworth, comb. nov. BASIONYM: *Sitanion brevifolium* J.G. Sm., Bull. U.S.D.A. Div.

Agrostol. Rep. Agrostol. 18:17 (1899). HOLOTYPE: United States. Arizona: Pima County, Tucson, 1892, Toumey 797 (US).

Elymus elymoides (Raf.) Swezey subsp. *californicus* (J.G. Sm.) Barkworth, comb. nov. BASIONYM: *Sitanion californicum* J.G. Sm., Bull. U.S.D.A. Div. Agrostol. Rep. Agrostol. 18:13 (1899). TYPE: United States. California: San Bernardino County, San Bernardino Mountains, 23 June 1894, Parish 3295 (US).

Elymus elymoides (Raf.) Swezey subsp. *hordeoides* (Suksd.) Barkworth, comb. nov. BASIONYM: *Sitanion hordeoides* Suksd., Werdenda 1:4 (1923). HOLOTYPE: United States. Washington: Spokane County, Spangle, 29 June 1916, Suksdorf 8705 (WS).

Elymus stebbinsii

As Michael Curto drew to my attention (oral comm. 1993), the holotype of *Agropyron parishii* Scribner & J.G. Smith var. *laeve* Scribner & J.G. Smith belongs in *Elymus trachycaulus* (Link) Gould subsp. *subsecundus* (Link) Gould. This means that names based on *A. parishii* var. *laeve* are synonyms of *E. trachycaulus* subsp. *subsecundus* and raised the question as to whether there is a taxon corresponding to the description of Scribner & Smith. After studying specimens from several herbaria, (Barkworth 1998) I concluded that there is such a taxon and named it *E. stebbinsii* Gould subsp. *septentrionalis*. It grows to the north and east of the Great Central Valley of California, not in San Diego County where the holotype of *Agropyron parishii* var. *laeve* was collected.

Elymus californicus

Elymus californicus (Bol.) Gould has traditionally been included in *Hystrix* as *H. californica* Bol. Inclusion of the type species for *Hystrix*, *H. patula* Moench [= *E. hystrix* L.] in *Elymus* meant that the generic placement of *H. californica* had to be reconsidered. In preparing the treatment of *Elymus* for the Jepson Manual (Barkworth 1993), I did not examine either species closely, largely because I was unaware of any compelling reasons for believing that they did not belong in *Elymus*. In particular, the general aspect and habitat of *E. californicus* seemed compatible with its inclusion in *Elymus*, if that genus included *E. hystrix* and *E. svensonii* G.L. Church. The only discordant note was Stebbins' (cited in Myers 1947) report that it was an octoploid, making it the only known octoploid in *Elymus* so far as I am aware. Löve (1980) initially reported that it had $2n = 28$, as is typical of North American species of *Elymus*, but later (Löve 1984), without comment, listed only $2n = 56$. More recently, Dr. Kevin Jensen (pers. comm., 1997) confirmed Stebbins' count of $2n = 56$.

Dewey (1983) considered *Elymus hystrix* an StH tetraploid, like most North American species of *Elymus*. He presented no direct evidence for this statement. The only cytological information for the species came from Church's (1967) crosses of *E. hystrix* with other eastern North American species of *Elymus*. Most of the crosses were unsuccessful, but a few yielded partially fertile hybrids. The most successful crosses were with *E. svensonii*. Unfortunately, *E. svensonii* is another genetically uncharacterized species.

Svitashov *et al.* (1997), using genome-specific repetitive DNA and RAPD markers, confirmed the presence of the H genome in *Elymus hystrix*, but only one of their three St genome-specific primers supported the presence of the St genome. They suggested that the St genome in *E. hystrix* may be substantially modified from that found in the other species of *Elymus* that they examined. They did not examine *Hystrix californica*, but did include two other species traditionally placed in *Hystrix*, *H. duthei* (Stapf) Bor and *H. komarovii* (Roshev.) Ohwi. Both responded to the markers used like the species of *Leymus* included in the study, not like unusual StH species.

Other studies also suggest that many species traditionally included in *Hystrix* are closer to *Leymus* than *Elymus*. Jensen & Wang (1997) transferred *H. coreana* (Honda) Ohwi to *Leymus* because both their cytological and molecular data (genome-specific RAPD markers) suggested that it belonged there. Their molecular data also supported transferring *H. californica*, but they left it in *Elymus* pending acquisition of cytological data. They did not comment on the morphology or ecology of either taxon, nor did they include *H. patula* in their study.

Baden *et al.* (1997) recognized *Hystrix* in the traditional sense. They argued that a) genomic information is of dubious value in phylogenetic analysis and b) that *Elymus* is undoubtedly polyphyletic so that removal of morphologically distinct groups would contribute to a better understanding of its relationships. They describe *Hystrix* as consisting of "loosely tufted species and though difficult to circumscribe precisely, the following combination of character states appears to set [*Hystrix*] apart from all other species of Triticeae 1) glumes either absent or reduced to tubercles or if present setaceous or subulate with carinate base (never flat), free, distinctly unequal, and inconspicuously 1(3)-nerved, never longer than the lemma (including awn), 2) large anthers (>2.5 mm), 3) spikelets disarticulating below the lowermost floret, and 4) lemma 4-7-nerved" (p. 450).

Of the six species that they recognized, three (*Hystrix patula*, *H. coreana*, and *H. sibirica* [Trautv.] Kuntze) had linear to broadly lanceolate leaves, the other three (*H. californica*, *H. duthei* [Stapf] Bor, and *H. komarovii* [Roshev.] Ohwi) having broad, lanceolate leaves. C-banding patterns for *H. patula*, *H. komarovii*, and *H. duthei* were distinct from those for *H. coreana*. The habitat summaries suggest that *H. coreana* and *H. sibirica* grow in rather open, rocky or sandy environments whereas the other four species grow in shadier locations within a forest and that *H. californica* and *H. duthei* tend to flower earlier in the season than the other four species.

The authors did not comment on *Elymus svensonii*, but it appears to fit the morphological criteria for *Hystrix*, nor did they provide any evidence that *Hystrix*, as they circumscribed it, is a monophyletic taxon. While genomic data cannot be used, by themselves, to determine the phylogenetic relationships among polyploid taxa, Svitashov *et al.* (1996) showed that they may be phylogenetically informative. At present, cytological and molecular data suggest that *Hystrix*, as recognized by Baden *et al.* (1997), is polyphyletic.

Because *Elymus hystrix* is the type species for *Hystrix*, its inclusion in *Elymus* precludes returning *E. californicus* to that genus. One could retain *E. hystrix* in *Hystrix*, as Baden *et al.* advocate, but one should then reconsider the generic affiliation

of *E. svensonii* and *E. diversiglumis* Scribnér & C.R. Ball. I believe that all three are best included in *Elymus*, but I am not completely convinced that *E. californicus* belongs there. On the other hand, I am not happy about transferring it to *Leymus* because it is so ecologically and morphologically distinct from that genus as I know it (Barkworth & Atkins 1984). My knowledge does not, however, include the Asian and South American species that Jensen & Wang (1997) and Dubcovsky *et al.* (1997) recently transferred to *Leymus*, nor am I familiar with the Asian species traditionally included in *Hystrix*. It seems best, therefore to leave *E. californicus* in *Elymus* pending more complete and multidisciplinary data on all the relevant species. The reason for this note is to draw attention to the anomalous aspects of *E. californicus* and to correct my report (Barkworth 1993) of an incorrect chromosome count for *E. californicus*.

Elymus glaucus

No nomenclatural changes are proposed for *Elymus glaucus* Buckley, but specimens examined as part of the study of *E. stebbinsii* (Barkworth 1998), indicated that anther length ranges from 2.0-4.6 mm in the species. I reexamined specimens at both extremes, but finally concluded that the upper limit had to be increased over the value I gave earlier (Barkworth 1993). I also found variation within individual specimens, in one case finding anthers of 3.6 and 4.6 mm on the same plant. Plants with shorter anthers showed less absolute variation. Snyder (1950) published a landmark paper on morphological variability in *E. glaucus*, but anther length was not one of the characters he studied.

Intergeneric Hybrids

The Triticeae is notorious for the ability of its members to hybridize, even between genera. Most of the intergeneric hybrids are highly sterile and very local in their distribution, but many have been given binomial names. The new combinations will permit the application of generic concepts adopted in the *Manual* to named, naturally occurring North American hybrids.

× *Elyhordeum californicum* (Bowden) Barkworth, *comb. nov.* BASIONYM: *Sitordeum californicum* Bowden, Canad. J. Bot. 45:722 (1967). SYNONYM: × *Elytesion californicum* (Bowden) Barkworth & D.R. Dewey, Amer. J. Bot. 72:772 (1985). Parents: *Sitanion jubatum* J.G. Sm. [= *Elymus multisetus* (J.G. Sm.) M.E. Jones] and *Hordeum jubatum* L.

× *Elyhordeum pilosilemma* (W.W. Mitchell & H.J. Hodgson) Barkworth, *comb. nov.* BASIONYM: × *Agrohordeum pilosilemma* W.W. Mitchell & H.J. Hodgson, Bull. Torrey Bot. Club 92:404 (1965). Parents: *Elymus macrourus* (Turcz.) Tzvelev [= *Agropyron sericeum* Hitchc.] and *Hordeum jubatum* L.

× *Leydeum* Barkworth, *gen. hybr. nov.*, *Leymus* Hochst. × *Hordeum* L.

× *Leydeum dutillyanum* (Lepage) Barkworth, *comb. nov.* BASIONYM: × *Elymordeum dutillyanum* Lepage, *Naturaliste Canad.* 84:97 (1957). Synonym: × *Leytesion dutillyanum* (Lepage) Barkworth in Barkworth & R.J. Atkins, *Amer. J. Bot.* 71:623 (1984). Parents: *Leymus mollis* (Trin.) Pilger and *Hordeum jubatum* L.

× *Leydeum piperi* (Bowden) Barkworth, *comb. nov.* BASIONYM: × *Elymordeum piperi* Bowden, *Canad. J. Bot.* 36:106-107 (1958). Parents: *Leymus triticoides* (Buckley) Pilger and *Hordeum jubatum* L.

UNPUBLISHED THESES

In working with North American Triticeae, some unpublished theses and dissertations have come to my attention. Because they contain useful information, I am listing them here so that others working on the tribe may locate them. In most cases, the reason that no publication resulted from the work is that publication was not necessary for the student's career after graduation. A few are available through UMI®; the remainder are, presumably, deposited in the libraries of the institutions concerned. The Intermountain Herbarium also has a copy of each. I would welcome information on additional unpublished theses and dissertations concerning the tribe.

Brooks, R.E. Intraspecific variation in *Elymus virginicus* (Gramineae) in the central United States. M.A. thesis, University of Kansas.

Collins, D.D. 1965. Ecological, biosystematic, and biochemical studies of species in the genus *Agropyron* Gaertn. native to Montana. Ph.D. dissertation, Montana State College.

Davies, R.S. 1980. Introgression between *Elymus canadensis* L. and *E. virginicus* L. (Triticeae, Poaceae) in south central United States. Ph.D. dissertation, Texas A&M University.

Godley, E.J. 1947. The variation and cytology of the British species of *Agropyron* and their natural hybrids. M.Sc. thesis, Cambridge University, United Kingdom.

Jensen, Jr., E.R. 1972. A taxonomic study of single spikelet *Elymus* species of western North America. Ph.D. dissertation, Utah State University.

Jozwik, F.X. 1966. A biosystematic study of the slender wheatgrass complex. Ph.D. dissertation, University of Wyoming.

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**ELYMUS WAWAWAIENSIS: A SPECIES HITHERTO CONFUSED WITH
PSEUDOROEGNERIA SPICATA (TRITICEAE, POACEAE)**

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ABSTRACT

Elymus wawawaiensis, spec. nov., is native to the valleys of the Snake River and its tributaries in Washington and northern Idaho. It resembles, and was originally confused with, *Pseudoroegneria spicata*, but differs morphologically in having narrower, acuminate to aciculate glumes, a more imbricate spike, and glabrate basal leaf sheaths. It differs cytologically in being an allotetraploid that combines the St and H genomes, like other North American species of *Elymus*, rather than an St diploid or autotetraploid, as are all species of *Pseudoroegneria*. *Elymus wawawaiensis* is considered a useful species for range improvement. A cultivar of the species, 'Secar', has been distributed by the U.S.D.A. under the name Snake River Wheatgrass.

KEY WORDS: *Elymus*, *Pseudoroegneria*, wheatgrass, Triticeae, Poaceae, plant geography

INTRODUCTION

Pseudoroegneria spicata (Pursh) A. Löve [= *Agropyron spicatum* (Pursh) Scribnér & J.G. Sm.] is a common grassland species in western North America. It grows in a wide range of communities, ranging from those of arid habitats where it occurs with *Poa secunda* J. Presl and *Artemisia tridentata* Nutt., to those of more mesic habitats dominated by *Pinus ponderosa* Lawson & C. Lawson or *Pseudotsuga menziesii* (Mirbel) Franco. Several years ago, Dewey (1982) noted that there appeared to be more than one biological element in *Pseudoroegneria spicata*. He commented in particular on a tetraploid accession from southeastern Washington (PI 285272) that differed in its general aspect and heat tolerance from most accessions of *Pseudoroegneria spicata* and formed sterile hybrids when crossed with typical accessions.

More extensive investigation (Carlson 1986), involving several populations of typical *Pseudoroegneria spicata* and additional populations resembling the distinctive accession revealed that the atypical populations are allotetraploids that combine the St genome of *Pseudoroegneria* with the H genome of wild barley (genome designations according to Wang *et al.* 1996). In this they resemble most native North American species of *Elymus* (Dewey 1984), but differ from typical plants of *P. spicata* (and other species of *Pseudoroegneria*), all of which are diploids or autotetraploids. There are no known species of *Elymus* that resemble the distinctive populations. These observations indicate that the distinctive populations should be treated as a new taxon. The purpose of this paper is to substantiate this assertion, characterize the new taxon, and provide it with an appropriate name. In anticipation of the conclusion, we refer to the new taxon as *Elymus wawawaiensis*. For lack of a valid scientific name, those working with it have, until now, referred to it as Snake River Wheatgrass (*e.g.*, Jones *et al.* 1991).

MATERIALS AND METHODS

The materials examined included plants from native populations of *Pseudoroegneria spicata*, *Elymus wawawaiensis*, and *E. lanceolatus* (Scribner & J.G Sm.) Gould, plants grown in uniform gardens from seed accessions obtained during the field studies or through the U.S.D.A., and herbarium specimens at OSC, US, UTC, and WS (herbarium codes from Holmgren *et al.* 1990). Plants of *P. spicata* may have lemmas with strongly divergent awns or lemmas that are essentially unawned. The two variants sometimes occur together, but uniform populations of one or other variant are common. The native populations used in this study consisted of uniformly awned or unawned plants. The seed accessions were also obtained from uniform populations. The emphasis in the morphological studies was on the comparison with *P. spicata* primarily because of the similarity between *P. spicata* and *E. wawawaiensis*, but also because of the Soil Conservation Service's [now the Natural Resources Conservation Service] interest in evaluating the biological diversity within *P. spicata*. We know of no species of *Elymus*, as we interpret that genus, that resembles *E. wawawaiensis*. *Elymus lanceolatus* was included because it grows in the vicinity and can form fertile hybrids with *E. wawawaiensis* although no naturally occurring hybrids were found.

Morphological Studies.--Plants from accessions of *Pseudoroegneria spicata*, *Elymus wawawaiensis*, and *E. lanceolatus* were grown at each of four sites: Evans Farm, Logan, Utah; Utah State University Deer Pen plots, Logan, Utah; Oregon State University Branch Experiment Station, Moro, Oregon; and Oregon State University greenhouse, Corvallis, Oregon. Each accession consisted either of seed from an undetermined number of wild plants growing at a single locality or of seed belonging to a recognized cultivar. The accessions included 37 of *Pseudoroegneria spicata*, 10 of *Elymus wawawaiensis*, 4 of *E. lanceolatus*, and 1 of an artificial cross between *P. spicata* and *E. lanceolatus*. The accessions of *E. lanceolatus* included two awned accessions, *i.e.*, *E. lanceolatus* subsp. *albicans* (Scribner & J.G. Sm.) Barkworth & D.R. Dewey, one of *E. lanceolatus* 'Sodar', and one of the breeding population that eventually gave rise to *E. lanceolatus* 'Schwendimar'.

Table 1. Morphological characteristics of diploid and tetraploid *Pseudoroegneria spicata*, *Elymus wawawaiensis*, and *E. lanceolatus*. Spikelet characters were measured on the spikelet at the third node. Data shown for continuous characters are range, mean and, in parentheses, standard deviation. The units used for length measurements are shown in the table. Vestiture was scored as none (0), sparse (1), moderate (2), dense (3); glume surface was scored as smooth (0), scabrous (1), very scabrous (2). Scores are presented parenthetically, preceded by the number of OTUs with that score. Asterisked characters were used in at least some of the discriminant analyses.

Character	Unawned	Diploid	Tetraploid	Combined	<i>E. wawa-waiensis</i>	<i>E. lanceolatus</i>
	<i>P. spicata</i>	<i>P. spicata</i>	<i>P. spicata</i>	<i>P. spicata</i>		
Number of OTUs	31	51	19	101	51	10
Culm						
Length (cm)*	27.7-75.6 55.1(12.7)	40.9-80.3 62.9(9.8)	45.7-79.6 62.5(7.3)	27.7-80.3 60.4(10.9)	45-100 70(12)	53.0-95.3 71.7(13.7)
Basal diameter (mm)*	1.0-2.6 1.4(0.4)	1.0-2.2 1.6(0.28)	1.2-2.4 1.6(0.3)	1.0-2.6 1.5(3.3)	1.0-1.9 1.5(0.3)	0.9-1.9 14.8(2.9)
Node (number)*	2-5 3.2(0.7)	2-8 3.4 (1.0)	3-4 3.5 (0.5)	2-8 3.4(0.85)	2-5 3.7(0.7)	3-4 3.5(0.5)
Top internode length (cm)*	20.7-41.6 30.8(5.5)	19.6-48.8 34.4(5.8)	21.3-42.0 34.6(6.0)	19.6-42.0 33.3(5.9)	17.0-47.8 30.4(6.3)	24.7-44.8 34.0(6.7)
Longest leaf						
Sheath length (cm)*	8.8-17.8 12.4(24.0)	8.2-20.3 12.8(2.6)	9.3-18.9 14.1(2.7)	8.2-20.3 12.9(2.6)	7.8-23.9 12.8(3.1)	9.0-16.2 12.0(2.1)
Sheath vestiture	1(2),30(3)	48(0),3(1), 1(3)	19(0)	67(0),3(1), 1(2),31(3)	48(0),3(1)	9(0),1(2)
Ligule length (mm)*	0.1-0.9 3.9(2.4)	0-1.0 0.37(0.23)	0.2-0.7 0.41(0.13)	0.0-1.0 0.4(0.21)	0.1-1.1 0.51 (0.27)	0.2-1.2 0.8(0.3)
Auricle length (mm)*	0.0-0.8 0.25(0.28)	0-1.1 0.24 (0.31)	0.0-0.9 0.3(0.3)	0.0-1.1 0.2(0.3)	0-1.2 0.16(0.25)	0-0.9 0.2(0.06)
Blade length (cm)*	9.1-27.0 18.6(3.9)	12.0-25.3 17.2(3.4)	16.0-27.2 19.9(2.7)	9.1-27.2 18.2(3.4)	8.5-28.2 17.2(4.0)	16.3-25.3 19.0(2.8)
Blade width (mm)*	0.9-6.1 27.6(11.6)	1.8-6.1 3.3(0.8)	2.4-5.1 3.5(0.8)	0.9-6.1 3.2(1.0)	1.7-4.2 2.9(0.5)	2.2-3.6 2.8(0.5)
Ribs in blade (number)*	8-21 12.9(3.3)	9-22 14.8(2.7)	12-21 15.4(2.6)	8-21 14.3(3.0)	9-19 14.1(2)	12-17 14(1.3)
Adaxial vestiture	1(2),30(3)	2(2),49(3)	19(3)	3(2),98(3)	1(0),4(1), 14(2),32(3)	10(3)
Abaxial vestiture	14(0),17(1)	42(0),9(1)	15(0),4(1)	81(0),20(1)	47(0),4(1)	9(0),1(1)
Flag leaf						
Sheath length (cm)*	13.5-26.4 18.3(2.9)	11.8-27.0 18.7(3.4)	13.6-26.2 19.3(3.5)	11.8-27.0 18.7(3.2)	12.1-26.6 19.1(3.8)	16.2-26.7 21.0(3.7)
Blade length (cm)*	1.7-24.7 12.3(4.3)	4.2-20.0 12.3(4.8)	8.3-26.9 15.2(4.7)	1.7-26.9 12.8(4.4)	2.3-17 9.9(1.5)	0.9-8.7 4.8(2.8)
Blade width (mm)*	0.7-5.9 2.3(0.9)	1.4-5.3 3.0(0.8)	2.1-4.7 3.2 (0.7)	0.7-5.3 2.8(0.9)	1.4-4.1 2.1(0.5)	0.9-2.9 1.7(0.6)

Table 1 (continued).

Character	Unawned	Diploid	Tetraploid	Combined	<i>E. wawawaiensis</i>	<i>E. lanceolatus</i>
	<i>P. spicata</i>	<i>P. spicata</i>	<i>P. spicata</i>	<i>P. spicata</i>		
Spike and spikelet						
Spike length (cm)*	10.5-20.8 15.4(2.5)	9.4-22.6 15.7(2.9)	11.2-21.7 15.0(2.8)	9.4-22.6 19(2.8)	6.6-17.9 11.2(2.7)	12.4-19.7 15.3(2.6)
Node (number)*	8-18 10.9(2.1)	8-17 11.4(2.2)	9-19 12.6(2.4)	8-19 11.5(2.2)	9-21 12.9(2.5)	12-16 14(1.3)
First spike internode length (mm)*	10-39 21.8(6.6)	11-39 22.6(6.8)	11-27 19.5(4.7)	10-39 22(6.4)	6-18 11(3.4)	11-19 15(3)
Third spike internode length (mm)*	10-19 14.7(2.6)	9-22 14.9(0.3)	9-16 13.0(2.0)	9-22 14.5(2.8)	5-13 8.3(1.8)	8-12 10(2)
Spikelet length (mm)*	11-24 18.2(2.6)	13-27 19.4(3.1)	15-22 19.25(2.2)	11-24 19(2.8)	9-21 14.5(2.8)	11-18 15(2.2)
Spikelet width (mm)*	1.9-7.0 4.0(1.3)	1.9-7.5 3.8(1.2)	2.2-6.5 4.3(1.4)	1.9-7.5 3.9(1.3)	2.0-8.5 1.4(0.3)	3.0-6.3 4.0(1.2)
Floret number per spikelet*	5-10 7.9(1.3)	5-11 7.6(1.5)	5-8 6.7(0.9)	5-11 7.5(1.4)	3-9 6.6(1.5)	5-9 7(1)
Second rachilla segment (mm)*	1.1-2.4 1.78(0.29)	1.0-2.2 1.6(0.3)	1.5-2.2 1.8(0.3)	1.0-2.4 1.7(0.3)	0.8-2.1 1.4(0.3)	1.2-1.6 1.4(0.13)
First glume length (mm)*	6.8-11.0 8.3(1.1)	5.8-11.2 7.9(1.4)	6.2-10.0 8.1(1.3)	5.8-11.2 8.0(1.3)	3.1-8.3 6.1(1.2)	4.3-8.6 6.6(1.1)
First glume width (mm)*	1.0-1.9 1.5(0.26)	1.0-2.1 1.5(0.3)	1.3-2.2 1.8(2.3)	1.0-2.2 1.5(0.3)	0.5-1.1 0.7(0.1)	0.8-1.3 1.1(0.2)
First glume awn length (mm)*	0.0-0.0 0.6(1.4)	0.0-8.0 0.63(0.8)	0.0-2.0 0.4(0.1)	0.0-8.0 0.4(0.1)	0.6-0 0.5(1.1)	0-0 0.4(0.05)
First glume veins (number)*	2-7 4.4(1.0)	3-6 4.3(0.7)	4-7 4.9(0.81)	2-7 4.4(0.8)	2-4 2.9(0.5)	3-5 3.3(0.7)
First glume adaxial vestiture	3(0),14(1), 14(2)	15(0),23 (1),13(2)	7(0),9(1), 3(2)	25(0),46 (1),30(2)	6(0),28(1), 17(2)	4(1),3(2), 3(3)
First glume abaxial surface	5(0),23(1), 3(2)	5(0),36(1), 10(2)	18(1),1(2)	10(0),77 (1),14(2)	1(0),27(1), 23(2)	3(0),6(1), 1(2)
Second glume length (mm)*	8.2-12.8 9.9(1.1)	6.7-13.1 8.9(1.4)	7.8-11.2 9.5(1.1)	6.7-13.1 9.3(1.4)	4.0-9.5 6.9(1.2)	5.2-9.1 7.1(1.0)
Second glume width (mm)*	1.2-2.3 1.7(0.3)	1.2-2.2 1.7(2.4)	1.4-2.2 1.9(0.2)	1.2-2.3 1.7(0.3)	0.6-1.2 0.8(1.1)	1.0-1.7 1.3(0.2)
Second glume awn length (mm)*	0.0-0.0 0.6(1.2)	0.0-5.0 0.7(1.1)	0.0-4.0 0.46(1.0)	0.0-5.0 0.5(0.1)	0.0-4.0 0.4(0.05)	0-1 0.4(0.05)
Second glume veins (number)*	3-8 5.1(1.1)	3-8 5.0(0.9)	5-8 5.8(0.9)	3-8 5.2(1.0)	3-5 3.5(0.6)	3-5 3.7(0.7)
Second glume adaxial vestiture	15(1),16(2)	12(0),23 (1),16(2)	5(0),10(1), 4(2)	17(0),48 (1),36(2)	4(0),24(1), 23(2)	4(1),4(2), 2(3)
Second glume abaxial surface	1(0),27(1), 3(2)	4(0),33(1), 14(2)	15(1),4(2)	5(0),75(1), 21(2)	28(1),23(2)	1(0),6(1), 3(0)
First lemma length (mm)*	8.8-13.3 10.5(1.3)	9.0-13.8 10.5(1.2)	9-13 11.2(1.0)	8.8-13.8 10.6(1.2)	7.2-11.7 9.3(1.1)	6.3-10.9 9.6(1.4)
First lemma width (mm)*	1.8-2.9 2.4(0.29)	1.5-3.0 2.3(3.0)	1.8-3.1 2.6 (0.3)	1.5-3.1 2.4(0.3)	1.4-2.8 2.1(0.2)	1.7-2.6 2.1(0.3)

Table 1 (continued).

Character	Unawned	Diploid	Tetraploid	Combined	<i>E. wawaiensis</i>	<i>E. lanceolatus</i>
	<i>P. spicata</i>	<i>P. spicata</i>	<i>P. spicata</i>	<i>P. spicata</i>		
First lemma abaxial vestiture	31(0)	49(0),2(1)	15(0),4(1)	95(0),6(1)	49(0),2(1)	3(2),7(3)
First lemma awn length (mm)*	0.0-1.0 0.03(0.18)	0-28.0 13.2(6.1)	0.0-16.0 8.1(4.6)	0.0-28.0 8.2(7.5)	0-19.5 17.4(2.9)	0-7.2 0.9(0.02)
Longest awn, lower spikelet*	0.0-1.0 0.03(0.18)	2.0-26.0 16.1(6.0)	0.0-26.0 12.4(5.8)	0.0-26.0 10.5(8.6)	0.0-25.0 15.6(5.0)	1.0-10.0 1.3(3.2)
Longest awn, upper spikelet*	0.0-9.0 0.3(1.6)	3.0-35.0 18.3(7.4)	0.0-24.0 15.7(6.8)	0.0-35.0 12.3(10.1)	0.0-26.0 18.3(5.0)	0.0-17.0 2.1(5.4)
Lemma awn angle*	0-10 0.3(1.8)	0-90 26.2(19.1)	0-35 12.4(10.2)	0-90 1.6(18.3)	0-80 22.7(15.2)	0-35 3.5(11)
Lemma awn longer than 3 mm ¹	0%	96%	84%	66%	100%	14%*
Palea length (mm)*	7.7-11.2 9.2(8.8)	7.3-11.3 9.3(0.9)	8.4-11.2 9.7(7.2)	7.3-11.3 9.3(8.8)	7.2-10.5 8.7(0.8)	5.1-9.9 8.5(1.5)
Palea width (mm)*	1.2-1.9 1.5(0.22)	0.9-2.1 1.6(0.3)	1.6-2.1 1.9(0.12)	0.9-2.1 1.7(0.3)	1.0-1.8 1.2(0.18)	1.1-1.8 1.3(0.2)
Palea adaxial vestiture	9(0),20(1), 2(2)	27(0),21 (1),3(2)	8(0),10(1), 1(2)	44(0),51 (1),6(2)	10(0),30 (1),11(2)	9(1),5(2)
Palea abaxial vestiture	28(0),3(1)	45(0),6(1)	15(0),4(1)	88(0),13(1)	26(0),17 (1),8(2)	2(0),4(1), 6(2),2(3)

*Lemma awns were scored as present if one of the lemmas had an awn more than 3 mm long. *Elymus lanceolatus* included subsp. *albicans*, an awned taxon.

The morphological characteristics of the accessions were examined using complete, mature culms from plants grown at the four sites. The number of samples per accession varied from one to ten, the average being 3.1. Except at Evans Farm, the size of the sample was determined by the number of plants that could be grown at each site. In sampling, a conscious effort was made to sample the full range of variation shown by each accession at a given site.

Forty-six morphological characters (Table 1) were selected for examination on the basis of existing treatments (Hitchcock 1951; Hitchcock 1969; Holmgren & Holmgren 1977) and study of native populations. These characters were examined on 166 culms representing 32 accessions grown from seed and 12 plants from a population about 0.5 mi up Wawawai Canyon from the Snake River (Table 2). Flowering culms were visually selected from the tallest third of the culms produced by the plant. Those selected had about average culm and spike lengths among this third. Cauline leaf measurements were made on the longest leaf below the flag leaf. This was usually the second leaf down, but was sometimes the first or third. The number of spikelets per spike was the mean of three tall culms; the number of florets per spikelet was the mean of three spikelets.

Table 2. Source of plants used for morphological studies of *Elymus* and *Pseudoroegneria*.

Source Location and Accession Number	Taxon	Number of OTUs	Ploidy level	Awn?
Columbia Plateau, Lincoln County, Washington (T40592)	<i>P. spicata</i>	5	Diploid	Unawned
Columbia Plateau, Lincoln County, Washington (T40593)	<i>P. spicata</i>	4	Diploid	Unawned
Columbia Plateau, Douglas County, Washington (T40590)	<i>P. spicata</i>	1	Diploid	Unawned
Along Columbia River, Okanogan County, Washington (D3363)	<i>P. spicata</i>	2	Diploid	Unawned
Colorado (7031)	<i>P. spicata</i>	2	Diploid	Unawned
Snake River Canyon, Wawawai, Whitman County, Washington (DS 120)	<i>P. spicata</i>	9	Diploid	Unawned
Palouse Prairie, Colton, Whitman County, Washington (D3363)	<i>P. spicata</i>	4	Diploid	Unawned
Logan, Cache County, Utah (D1252)	<i>P. spicata</i>	4	Diploid	Unawned
New Meadows, Adams County, Idaho (D2837)	<i>P. spicata</i>	8	Diploid	Awned
Slopes above Snake River, Hellers Bar, Asotin County, Washington (DS 117)	<i>P. spicata</i>	5	Diploid	Awned
Decker, Montana (D2838)	<i>P. spicata</i>	4	Diploid	Awned
Custer, Idaho (BB1600)	<i>P. spicata</i>	4	Diploid	Awned
Strevel, Utah (D2836)	<i>P. spicata</i>	2	Diploid	Awned
Rocky slopes above Grande Ronde River, Wallowa County, Oregon	<i>P. spicata</i>	15	Diploid	Awned
Open <i>Pinus ponderosa</i> forest, Avon, Montana	<i>P. spicata</i>	5	Diploid	Awned
Grassy valley (old Lake Missoula Lake bed), Deerlodge, Montana	<i>P. spicata</i>	4	Diploid	Awned
Open <i>Pinus ponderosa</i> forest, Gold Creek, Montana	<i>P. spicata</i>	5	Diploid	Awned
Palouse Prairie, Steptoe Butte, Whitman County, Washington	<i>P. spicata</i>	15	Tetraploid	Awned
<i>Pinus ponderosa</i> woodland, Clearwater, Idaho (T7681)	<i>P. spicata</i>	4	Tetraploid	Awned

Table 2 (continued).

Source Location and Accession Number	Taxon	Number of OTUs	Ploidy level	Awn?
Riggins, Idaho County, Idaho (D2842)	<i>E. wawawaiensis</i>	2	Tetraploid	Awned
Wawawai, Whitman County, Washington (DS 122)	<i>E. wawawaiensis</i>	5	Tetraploid	Awned
Penawawa, Whitman County, Washington	<i>E. wawawaiensis</i>	10	Tetraploid	Awned
New Meadows, Idaho (D2841)	<i>E. wawawaiensis</i>	3	Tetraploid	Awned
Howell Canyon, Whitman County, Washington (D2843)	<i>E. wawawaiensis</i>	4	Tetraploid	Awned
Central Ferry, Washington	<i>E. wawawaiensis</i>	5	Tetraploid	Awned
Dry coulée, Washtucna, Washington	<i>E. wawawaiensis</i>	5	Tetraploid	Awned
Central Ferry, Washington	<i>E. wawawaiensis</i>	5	Tetraploid	Awned
Wawawai, Whitman County, Washington [OTUS collected in the field and pressed]	<i>E. wawawaiensis</i>	12	Tetraploid	Awned
Artificial hybrid; BB0138	<i>P. spicata</i> × <i>E. lanceolatus</i>	4		
Canada	<i>E. lanceolatus</i> subsp. <i>albicans</i>	2	Tetraploid	
Sherman County, Oregon (T21076)	<i>E. lanceolatus</i>	3	Tetraploid	
Grand County, Oregon	<i>E. lanceolatus</i> cv. <i>Sodar</i>	1	Tetraploid	
Wyoming	<i>E. lanceolatus</i> subsp. <i>griffithsii</i>	4	Tetraploid	

Discriminant analysis was used to determine which continuous morphological characters would be most valuable in identifying the group to which an OTU belonged. The groups used were a) unawned, diploid *Pseudoroegneria spicata*, b) awned, diploid *P. spicata*, c) tetraploid *P. spicata* (almost all of which were awned), d) *Elymus wawawaiensis*, and e) *E. lanceolatus*. Data from the artificial hybrid were not included (here and elsewhere, "awned" and "unawned" refers to the lemmas, not the glumes). Thirty-seven characters were used in the discriminant analysis (Table 1). The excluded characters were discontinuous with few alternative states.

Table 3. Pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions.

First Function		Second Function		Third Function	
Second glume width	0.669	Lower lemma awn	0.678	Lowest lemma awn	0.385
First glume width	0.571	Upper lemma awn	0.658	Flag blade length	0.285
First glume vein	0.352	Lemma awn angle	0.325	Spike length	-0.227
Second glume vein	0.335	Lowest lemma awn	0.292	Second glume length	0.183
Palea width	0.320	Flag blade width	0.231	Lemma awn angle	-0.160
Second glume length	0.316	Palea width	0.152	Second glume vein	0.159
First internode length	0.302	Cauline blade ribs	0.144	First glume vein	0.149
Spikelet length	0.262	Second glume awn	0.141	Culm diameter	-0.141
First glume length	0.253	Culm diameter	0.140	Spikelet width	0.139
Spike length	0.234	Cauline blade width	0.140	Cauline sheath	0.119

Classification tree analysis was used to explore the ability of the discontinuous and continuous characters for distinguishing between *Elymus wawawaiensis* and the three *Pseudoroegneria spicata* groups. This procedure resembles discriminant analysis in that it works from predefined groups, but it looks for individual characters that will, if used in sequence, most effectively place the objects into the correct group, *i.e.*, it is a divisive method of hierarchical cluster analysis with only one character being used to split an existing cluster. It can be used with both continuous and discontinuous data. *Elymus lanceolatus* was excluded from the analysis because the number of OTUs in the study was too low.

Excel (Microsoft 1997) was used to generate summary statistics for each group, SPSS version 7.5.1 for discriminant analysis (SPSS 1997), S-plus4 for classification tree analysis (MathSoft 1997), and NTSYS-pc (Rohlf 1993) to produce three dimensional projections.

Cytological studies.--Somatic chromosome counts were already available for approximately 110 accessions of *Pseudoroegneria spicata*, *Elymus lanceolatus*, and *E. wawawaiensis*. Counts for an additional 152 populations of these taxa were obtained as part of Carlson's (1986) study. The counts were obtained from root tips that had been pre-treated in ice water for 24 hr, hydrolyzed in 1N HCl at 60°C for 10 min, and stained with Feulgen. For polyploid plants, metaphase 1 of meiosis was also examined using pollen mother cells stained with acetocarmine. In autotetraploid *P. spicata*, quadrivalents predominate (Dewey, oral comm., 1986) consequently the

absence of quadrivalents was interpreted as meaning that the plant concerned was an allotetraploid.

Distributional studies.--The morphological characters identified as distinguishing *Elymus wawawaiensis* were used to identify specimens in OSC, US, WS, and UTC. These data, together with the collection data for the seed accessions, were used to determine the geographic and ecological distribution of the species.

RESULTS AND DISCUSSION

Field observations.--Carlson located several cytologically unexamined populations that would have keyed to *Pseudoroegneria spicata* (or *Agropyron spicatum*) in existing floras. These were tentatively identified as being either StH allotetraploids or St diploids or autotetraploids on the basis of their overall morphology. Subsequent cytological examination demonstrated that the allotetraploids had been correctly identified, but that diploid and autotetraploid populations could not be distinguished from each other.

Morphological studies.--Table 1 summarizes the morphological data obtained. Because the goal of this paper is to establish the need to recognize *Elymus wawawaiensis*, discussion of the data for *Pseudoroegneria spicata* will be presented elsewhere.

The characters that differentiate most clearly between *Pseudoroegneria spicata* and *Elymus wawawaiensis* are glume width and, to a lesser extent, glume venation, rachis internode length, and glume length (Table 1; Figs. 1-3.). The glumes of *E. wawawaiensis* are also somewhat stiffer and more sharply pointed than those of *P. spicata*. Seedlings of the two species can also be distinguished because those of *E. wawawaiensis* have pubescent leaf sheaths that become glabrous as the plant matures, whereas as seedlings of *P. spicata* are glabrous even in seedlings. In this respect, seedlings of *E. wawawaiensis* resemble those of *E. lanceolatus*.

Almost all specimens of *Elymus wawawaiensis* are awned. There were three exceptions among the OTUs, but only one was completely unawned, one of the other two having some shortly (3-6 mm) awned lemmas, and the other having some lemmas with normal (10-18 mm) awns. In the minimally awned plants, the longer awns are on the distal lemmas of a spikelet, as is the case in minimally awned plants of *Pseudoroegneria spicata*. The accessions of *E. wawawaiensis* that produced unawned OTUs came from populations that had populations of both unawned *P. spicata* and unawned *E. lanceolatus* in the vicinity.

Analysis of the F₂ generation of a cross between *Elymus wawawaiensis* and unawned plants of *E. lanceolatus* demonstrated that the awn character in these taxa is controlled by a single major gene and that the unawned allele is dominant (T. Jones, in litt., 1998). Such hybrids are easily produced, although few become established under natural conditions. Indeed, the only suggestion that any were present in the populations studied was the presence of unawned specimens in plants raised from

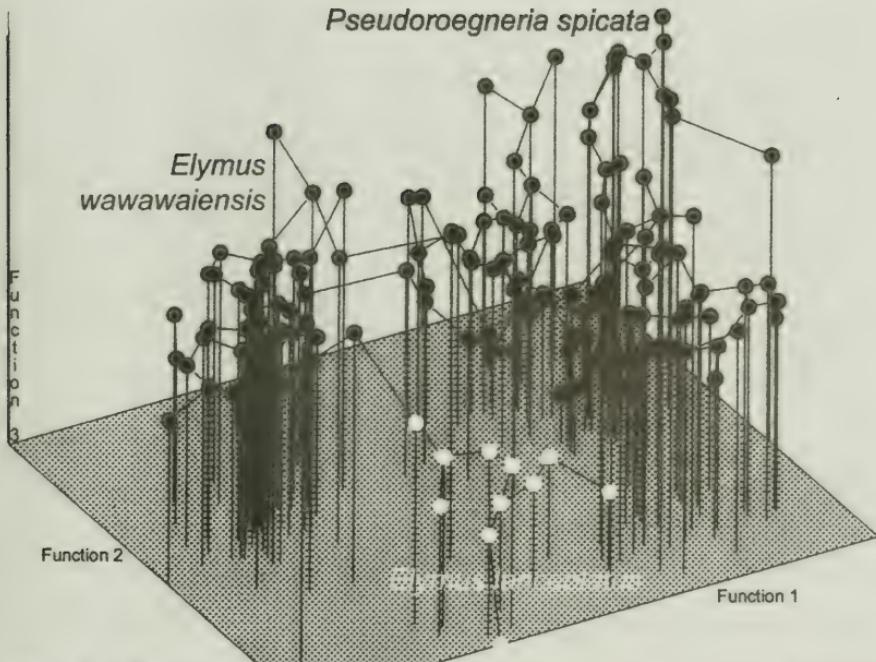


Fig. 1. Position of OTUs on first three discriminant axes

Figure 1. Distribution of *Elymus wawawaiensis*, *E. lanceolatus*, and the three *Pseudoroegneria spicata* groups in the plane defined by the first three discriminant functions. The first function is on the longest axis, the third function on the vertical axis. Light gray - *E. lanceolatus*; dark gray - *E. wawawaiensis*; black - *P. spicata*.

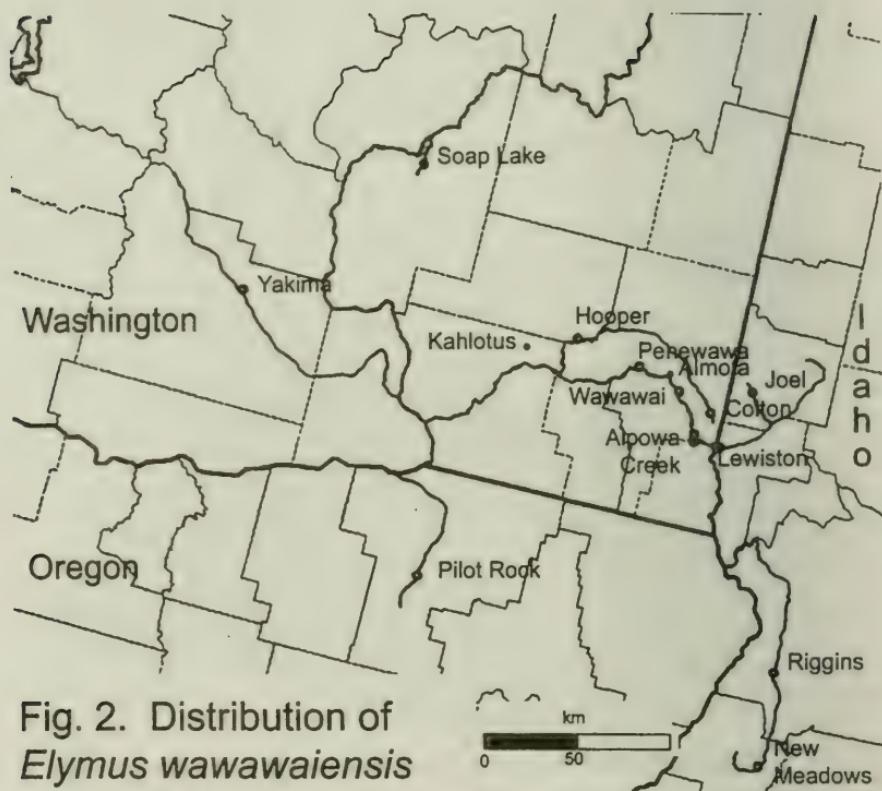


Fig. 2. Distribution of *Elymus wawawaiensis*

Figure 2. Distribution of *Elymus wawawaiensis*.



Figure 3. Holotype of *Elymus wawawaiensis*.

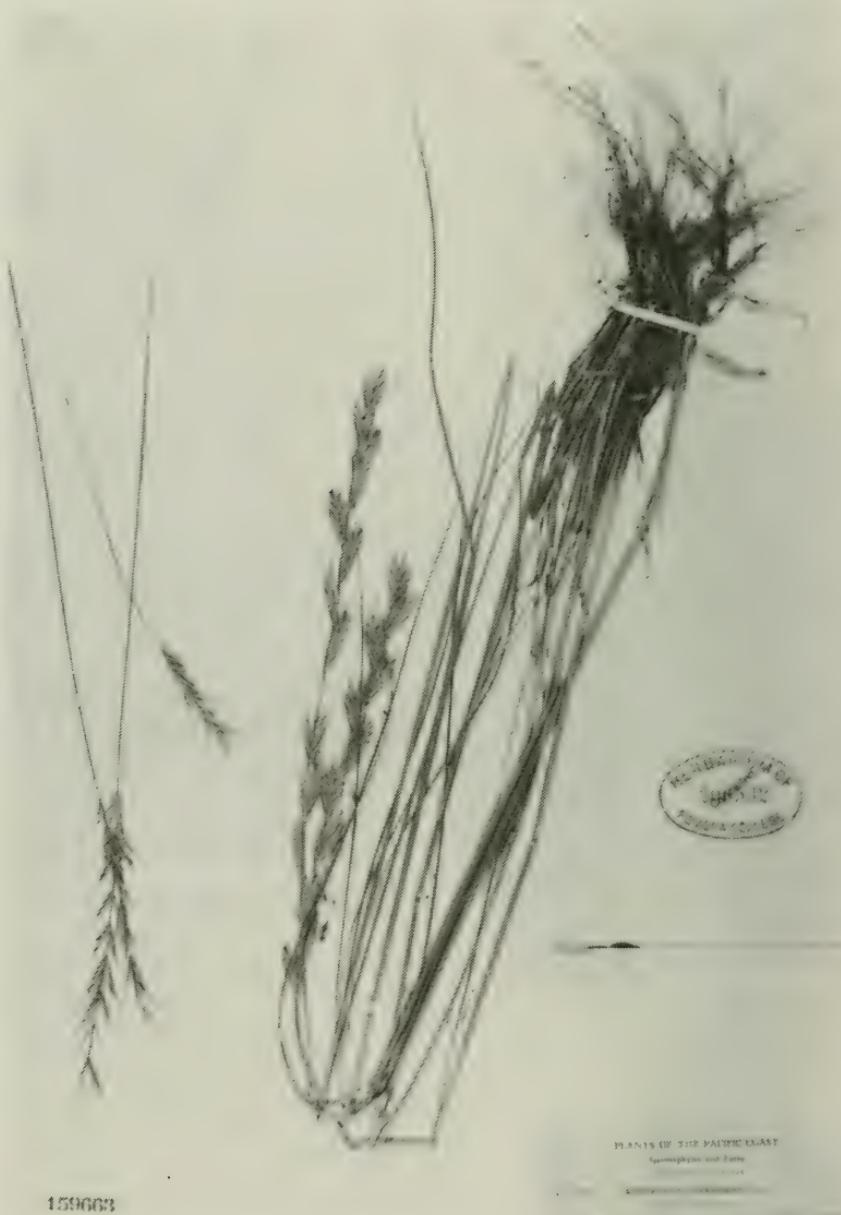


Figure 4. Representative of awned *Pseudoroegneria spicata*.

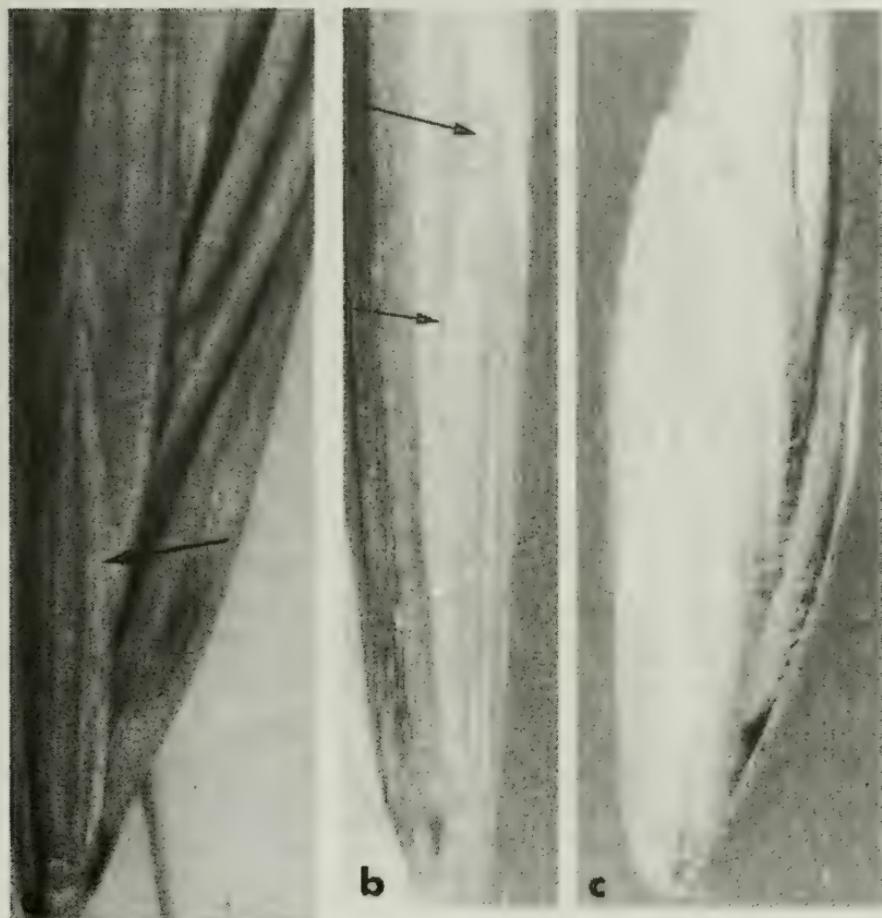


Figure 5. First glume of a) *Elymus wawawaiensis* b) *Pseudoroegneria spicata*, and c) *E. lanceolatus*. Arrows point to the edge of the glume.

seeds obtained in the wild. It is also possible that the unawned *E. wawawaiensis* plants reflect introgression from the unawned *Pseudoroegneria spicata* plants in the vicinity because a few triploid hybrids were found in mixed populations of the two taxa. Further study is needed to determine which of the two scenarios for the origin of the unawned *E. wawawaiensis* plants is correct.

Discriminant analysis.--The *Pseudoroegneria spicata* OTUs were placed in three different groups: unawned diploids, awned diploids, and tetraploids (most of which are awned), to determine whether the morphological characters used could be used to distinguish *Elymus wawawaiensis* even from those plants of *P. spicata* that most resembled it. The addition of the *E. lanceolatus* OTUs brought the number of groups compared to 5. Only six of the 37 characters included in the discriminant analyses had means that showed no significant difference (using $P=0.05$ as the level of significance) among the five groups. They were flag leaf sheath length, auricle length, caudine sheath length, spikelet length, first glume awn length, and number of caudine nodes.

Discriminant analysis clearly separated the *Elymus wawawaiensis* OTUs from those in the other four groups (Figure 1). When the identification of each OTU was cross-validated by evaluating its identification using discriminant functions based on data from all but the OTU of interest, four of the 152 OTUs were considered "misidentified". Three of the "misidentifications" were between the *Pseudoroegneria spicata* groups, but one *E. wawawaiensis* OTU was placed in the awned diploid *P. spicata* group. The highest correlation between the first discriminant function and the morphological characters was with glume width (Table 3).

With classification tree analysis, the first split was based on second glume width and separated the *Elymus wawawaiensis* OTUs from the three *Pseudoroegneria spicata* groups (the *E. lanceolatus* OTUs were omitted because there were so few of them). There was only one error in the placement of the *E. wawawaiensis* OTUs.

Distributional data.--Most collections of *Elymus wawawaiensis* are from coulees and side canyons of the Snake River and its tributaries in southeastern Washington and northern Idaho (Figure 2). At many sites, *E. wawawaiensis* grows in mosaics with unawned forms of *Pseudoroegneria spicata*. At such sites, *E. wawawaiensis* is easily distinguished by its awns.

There are a few records of *Elymus wawawaiensis* from localities at some distance from the Snake River and its tributaries. These may represent natural populations, but it is also possible that they reflect the distribution of seeds from the population near Wawawai, possibly by Charles V. Piper who founded the herbarium at Washington State Agricultural College (now Washington State University) in 1890, leaving to join the U.S.D.A.

CONCLUSIONS

The atypical populations of *Pseudoroegneria spicata* that Dewey referred to differ from both the diploid and autotetraploid plants of typical *P. spicata* in having narrower, sharper glumes with fewer veins and shorter, more compact spikes, as well as in being allotetraploids. The morphological differences between typical *P. spicata* and the allotetraploid plants are sufficiently great that there is rarely a problem in distinguishing between the two, either in the field or the herbarium.

The values for the distinguishing characters in *Elymus wawawaiensis* are either above or below those of *Pseudoroegneria spicata* and *E. lanceolatus*. This tends to refute the possibility that *E. wawawaiensis* consists of introgressants between the other two taxa. Hybrids may have values that exceed the extremes observed in their parents, but there are no tetraploid populations of *P. spicata* in the vicinity of *E. wawawaiensis*. This does not preclude the possibility that *E. wawawaiensis* originated when an unreduced gamete of diploid *P. spicata* crossed with *E. lanceolatus* but, based on the current distribution of awned and unawned plants of *P. spicata*, one would expect the unawned allele to be present to a significant extent in *E. wawawaiensis* if this were the case. It is, of course, possible that unawned hybrids are rapidly eliminated by selection for the advantages associated with awns. These include greater likelihood that the seeds will be moved to favorable microsites and lodge at the best angle for germination (Peart 1979).

Elymus wawawaiensis and *E. lanceolatus* are not genetically isolated from each other. Hybrids between the two are easy to produce, meiotically regular, and have only slightly depressed fertility. Despite this, the only evidence for the existence of natural hybrids was the discovery of unawned plants among those grown from seed obtained in the wild, a result that could also reflect introgression from unawned populations of *Pseudoroegneria spicata* growing in the vicinity. Although *E. lanceolatus* and *E. wawawaiensis* grow in the same region, they occupy different habitats, *E. wawawaiensis* occupying slopes with high daytime temperatures and shallow, rocky soils whereas the *E. lanceolatus* populations are largely confined to sandy soils, particularly older sand dunes, in the vicinity. The distance between the two kinds of habitat may preclude pollen transfer between natural populations of the two taxa. Alternatively (or additionally), hybrid seed may form but the seedlings be unable to become established under natural conditions. Whatever the reasons, the data suggest that *E. wawawaiensis* constitutes a taxon that is distinct from *E. lanceolatus*, although genetically similar to it. Because the new taxon has a similar origin to other species included in *Elymus*, as we interpret that genus, we include it in that genus rather than in *Pseudoroegneria*.

ELYMUS WAWAWAIENSIS J. Carlson & Barkworth, *spec. nov.*
HOLOTYPE: U.S.A. Washington: Whitman County, Wawawai, June 1902,
C.V. Piper 3954 (US 1017771) (Figure 3). Paratypes: U.S.A., Idaho, Nez Perce
County, Lewiston (US 221707); U.S.A., Oregon, Umatilla County, Pilot Rock
(US 1017821); U.S.A., Washington, Okanogan County, Okanogan (US
1017759); U.S.A. Washington, Whitman County, Almota (US 23054); U.S.A.,
Washington, Whitman County, Cow Creek (US 1017790).

Gramina perennia, caespitosa. Culmi 15-130 cm alti. Vaginae foliorum basiliū plerumque modice pubescentes juvenes, glabrae maturae, marginibus perspicue ciliatis. Vaginae foliorum caulinorum 6-18 cm longae, glabrae (raro pubescentes sparsim); laminae usque 26 cm longae, 2-5 mm latae, pagina adaxiali plerumque dense pubescenti, solum raro sparsim pubescentes; folia superne perpendicularia in siccitatibus. Spicae 6-20 cm longae, erectae vel erectiusculae, non rumpentes ut maturae; plurima internodia minus quam 1 cm longa. Spiculae solitariae, plus minusve imbricatae, 1-2 cm longae, cum 4-10 flosculis. Glumae 4-10 mm longae, 0.6-1.3 mm latae, lanceolatae ad usque aciculares, cum 1-3 venis; lemmæ 7-12 mm longae, rasiles usque ad scabellas, marginibus sparsim pubescentibus prope basin, aristatae; arista sola 10-25 mm longa, divergentes usque ad squarrosus reflexæ ubi maturæ; paleæ duplicarinatae, sparsim vel modice strigulosæ in paginae adaxiali, sparsim strigulosæ in pagina abaxiali apicem versus; antheræ 3-6 mm longæ. $2n = 28$.

Plants perennial, caespitose. Culms 15-130 cm tall. Basal leaf sheaths usually moderately pubescent when young, glabrous when mature, the margins not evidently ciliate. Cauline leaf sheaths 6-18 cm long, glabrous (rarely sparsely pubescent); blades to 26 cm long, 2-5 mm wide, the adaxial surface usually densely pubescent, only rarely sparsely pubescent; flag leaves perpendicular to the stem under drought stress. Spikes 6-20 cm long, erect to somewhat nodding, not disarticulating at maturity; most internodes less than 1 cm long. Spikelets solitary, more or less imbricate, 1-2 cm long, with 4-10 florets. Glumes 4-10 mm long, 0.6-1.3 mm wide, lanceolate to acicular, 1-3 veined; lemmas 7-12 mm long, smooth to slightly scabrous, sparsely pubescent along the margins near the base, awned; awn 10-25 mm long, divergent to squarrose at maturity; paleas 2-keeled, sparsely to moderately strigulose adaxially, sparsely strigulose abaxially towards the tip; anthers 3-6 mm long. $2n = 28$. Genomes StH.

Field and herbarium studies show that *Elymus wawawaiensis* is limited to the coulees and reaches of the lower Snake River drainage, *i.e.*, along the breaks and tributaries of the Salmon, Snake, and Yakima rivers in northern Idaho, northeastern Oregon, and southeastern Washington (Figure 2), habitats initially created during the Spokane and Bonneville floods (Allen *et al.* 1986). The highest concentration of the populations is found along the Snake River between its confluence with the Salmon River and Penewawa, suggesting that the progenitor seedlings became established on the scoured canyon walls in the region and then spread downstream, probably during the Pleistocene. The species will become more widespread through distribution of 'Secar', a cultivar developed by the U.S.D.A. for soil conservation in areas with shallow, rocky soils. The cultivar will probably hybridize with both *E. lanceolatus* and *E. trachycaulus* (Link) Gould if these species are in the vicinity, but whether the hybrids will become established is problematical.

Elymus, even when restricted to allopoloids that combine the St genome with one or more other genomes, is a morphologically and ecologically diverse genus. North American species combine the St genome with the H genome from wild barley and range from the strongly caespitose, short-lived, long awned *E. elymoides* (Raf.) Swezey to the rhizomatous, long-lived, unawned *E. lanceolatus*. Given their morphological, ecological, and geographic diversity of StH species (they extend from Europe to North and South America), it has always been highly improbable that they had a single tetraploid ancestor in common, but the tools for investigating their

ancestry have only recently been developed. Svitashov *et al.* (1996) demonstrated that the StH species are polyphyletic, but their sample size was too small to provide reliable information on clades within the species group. *Elymus wawawaiensis* may have originated independently from other North American species of *Elymus*, or it may be derived from another species, possibly through backcrossing with *Pseudoroegneria spicata*. At present there is not enough information available to select between these two scenarios.

ACKNOWLEDGMENTS

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